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# The British Mycological Society

*(Recognosce notum, ignotum inspice)*

## TRANSACTIONS

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Edited by

J. RAMSBOTTOM, B. F. BARNES and H. WORMALD

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## THE LYNDHURST SPRING FORAY

*May 26th-30th, 1933*

By E. M. WAKEFIELD

THE Spring Foray in 1933 was held at Lyndhurst, in the New Forest, from May 26th to May 30th, with headquarters at the Crown Hotel. After a month of fine, dry weather it seemed unlikely that very many of the larger fungi would be found, and in fact, as will be seen from the list, this foray proved to be the poorest in the records of the Society for fungi of any kind.

Rain fell on the first day of the foray, but this was too late to have any influence on the number of species occurring during the weekend; and as it was continuous and heavy the only result was that it put an early end to collecting on that day.

The first excursion on Saturday, May 27th, was over ground on either side of the road between Lyndhurst and Brockenhurst. In a normal season this should have been good, but very little was obtained, and even the bravest were at last obliged to give up owing to the rain.

On the following day the weather was better, and after a little exploration in the garden of the hotel the party set out in the direction of Lyndhurst Road railway station. In some damp spots at the side of the road various rusts and other microfungi were found, and small copses yielded a few of the larger fungi to increase the list. Monday, May 29th, was spent in the forest region to the west of Lyndhurst, along Highland Water and towards Mark Ash. The ground here was so barren, however, that after lunch a few of the party went by car to Ringwood, and explored the riverside there. The species found in the neighbourhood of Ringwood are indicated separately in the following list, but the other localities visited were all so close to Lyndhurst that they are treated as one.

In the evening on Saturday, May 27th, Dr R. Butcher gave an interesting talk on "Polysaprobic organisms and their value as indicators of the condition of waters." The paper was illustrated by photographs showing typical examples of growths found in polluted waters.

A business meeting was held on the Sunday evening to elect new members and to choose the locality for the Spring Foray in 1934. Considerable discussion on the latter subject led to no definite decision, but the Secretary was asked to make enquiries about Woodhall Spa and Sherwood Forest; the final decision was left to the Council.

It has since been ascertained that the former place is not very promising, and further, a definite invitation has been received from Mr E. M. Day to visit Stroud. It has been decided therefore to hold the 1934 Spring Foray at Stroud, in Gloucestershire.

*Complete List of Species gathered during the Foray*

HYMENOMYCETES

*Russula cyanoxantha* (Schaeff.) Fr.  
*Collybia leucomyosotis* Cooke & Smith  
*Marasmius dryophilus* (Bull.) Karst., *oreades* (Bolt.) Fr.  
*Panus stypticus* (Bull.) Fr.  
*Nolanea proletaria* Fr.  
*Pholiota adiposa* Fr.  
*Bolbitius titubans* (Bull.) Fr.  
*Inocybe lacera* Fr., *near Beaufieu*  
*Stropharia semiglobata* (Batsch) Fr.  
*Polyporus betulinus* (Bull.) Fr., *adustus* (Willd.) Fr.  
*Fomes ferruginosus* (Schrad.) Mass.  
*Ganoderma applanatum* (Pers.) Pat., *laccatum* (Kalchbr.) Rea  
*Polystictus versicolor* (Linn.) Fr.  
*Trametes gibbosa* (Pers.) Fr.  
*Daedalea quercina* (Linn.) Fr.  
*Merulius lacrymans* (Wulf.) Fr.  
*Irpea obliqua* (Schrad.) Fr.  
*Acia fuscoatra* (Fr.) Pat.  
*Odontia papillosa* (Fr.) Bres.  
*Grandinia farinacea* (Pers.) Bourd. & Galz.  
*Stereum hirsutum* (Willd.) Fr., *spadiceum* (Pers.) Fr.  
*Hymenochaete corrugata* (Fr.) Lév.  
*Corticium praetermissum* (Karst.) Bres., *porosum* B. & C., *roseocremeum* Bres.  
*Peniophora hydnoides* Cooke & Mass.  
*Exidia Thuretiana* (Lév.) Fr., *nucleata* (Schw.) Rea  
*Dacryomyces deliquescent* (Bull.) Duby

UREDINALES

*Puccinia Anemones* Pers., *Violae* (Schum.) DC., *Circaeae* Pers., *expansa* Link,  
*Taraxaci* Plowr., *Hypochoeridis* Oud., *Veronicae* Schroet., *coronata* Corda  
 (aecidium on *Rhamnus Frangula*), *Caricis* (Schum.) Rebent. (aecidium on  
*Urtica*), *Phragmitis* (Schum.) Koern. (on *Phragmites* and aecidium on *Rumex*),  
*Ringwood*

*Phragmidium mucronatum* (Pers.) Schlecht.  
*Kuehneola albida* (Kuehn.) Magn.  
*Coleosporium Melampyri* (Rebent.) Kleb.  
*Melampsorella Sympyti* (DC.) Bubák, *Ringwood*

USTILAGINALES

*Urocystis Anemones* (Pers.) Wint.  
*Entyloma microsporum* (Ung.) Schroet.

PYRENOMYCETES

*Sphaerotheca pannosa* (Wallr.) Lév.  
*Podosphaera Oxyacanthae* (DC.) de Bary  
*Epichloe typhina* (Pers.) Tul.

## The Lyndhurst Spring Foray

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*Lasiosphaeria hirsuta* (Fr.) Ces. & de Not., on *Fagus*  
*Rosellinia velutina* Fuck.  
*Melanomma pulvis-pyrius* (Pers.) Fuck., on *Fagus*, *fuscidulum* Sacc.  
*Ceratostomella* (?) *vestita* Sacc. on *Fagus*  
*Calyculosphaeria tristis* (Fuck.) Fitzp., on *Fagus*  
*Stigmataea Robertiana* Fr.  
*Mycosphaerella maculiformis* (Fr.) Schroet.  
*Venturia Runicis* (Desm.) Wint., *inaequalis* Aderh.  
*Diaporthe eres* Nits. on *Ilex*, *leiphaemia* (Fr.) Sacc. on *Quercus*  
*Eutypa spinosa* (Pers.) Tul. on *Fagus*, *Acharia* Tul. on *Fagus* and *Hedera*  
*Melogramma spiniferum* (Wallr.) de Not. on *Fagus*  
*Diatrypella querina* (Pers.) Fr.  
*Diatrype Stigma* (Hoffm.) de Not.  
*Hypoxyylon semiimmersum* Nits. on *Quercus*, *serpens* (Pers.) Fr. on *Fagus*, *cohaerens* (Pers.) Fr. on *Fagus*, *fuscum* (Pers.) Fr. on *Corylus*, *rutilum* Tul. on *Fagus*, *coccineum* Bull. on *Fagus*  
*Ustulina vulgaris* Tul. on *Fagus*  
*Xylaria Hypoxylon* (Linn.) Grev.

## HYSTERIALES

*Hysterium angustatum* A. & S. on *Fagus*.  
*Gloniopsis curvata* A. & S. on *Fagus*

## DISCOMYCETES

*Aleuria umbrina* Boud.  
*Ciliaria scutellata* (Linn.) Quél.  
*Taphrina deformans* (Berk.) Tul. on Almond, *Tosquinetii* (West.) Magn. on *Alnus*, *Potentillae* (Earl.) Johans. on *Potentilla Tormentilla*  
*Bulgaria inquinans* (Pers.) Fr.  
*Chlorosplenium aeruginosum* (Oeder.) de Not.  
*Dasyscypha virginea* (Batsch) Fuck.  
*Arachnopeziza aurelia* (Pers.) Fuck., *Beaulieu*  
*Mollisia cinerea* (Batsch) Karst.  
*Stegia Ilicis* Fr.  
*Colpoma quercinum* (Pers.) Wallr.  
*Rhytisma acerinum* (Pers.) Fr.

## PHYCOMYCETES

*Synchytrium Taraxaci* de Bary & Wor.  
*Plasmopara nivea* Schroet. on *Aegopodium*  
*Bremia Lactucae* Regel on *Lapsana* and *Leontodon*  
*Peronospora calotheca* de Bary on *Galium Aparine*, *Myosotidis* de Bary on *Myosotis*

## DEUTEROMYCETES

*Phyllosticta hedericola* Dur. & Mont.  
*Actinonema Rosae* (Lib.) Fr.  
*Oidium alphitoides* Griff. & Maubl.  
*Botrytis cinerea* Pers. on *Cheiranthus Allionii*  
*Trichoderma viride* Fr.  
*Ramularia Primulae* Thuem.  
*Isaria farinosa* (Dicks.) Fr.

## THE NEWCASTLE FORAY

September 18th-23rd, 1933

By E. M. WAKEFIELD

THE thirty-seventh Autumn Foray and Annual General Meeting was held at Newcastle-on-Tyne during the week September 18th-23rd. By kind permission of Prof. J. W. Heslop Harrison and the Council of the College, headquarters were in the Department of Botany of Armstrong College. Here books and microscopes were available, and ample space for work and for the exhibition of specimens.

The attendance was smaller than is usual at autumn meetings, no doubt owing to the certainty that after the long, dry summer there would be very few fungi to be found. About twenty members and friends assembled on the Friday evening, and were received by Prof. and Mrs Harrison in the Department of Botany.

On the Tuesday morning, September 19th, an early start was made by train for Alnwick, where Hulne Park was explored. The ground here was fairly damp in places, and the number of fungi found, though very unlike a normal season's haul, was quite cheering to those who came expecting nothing. Almost at once the debris beneath a large beech yielded numerous specimens of *Xylaria carpophila* in good condition. *Lepiota Bucknallii*, *Tricholoma acerbum*, *Hebeloma subsaponaceum*, *Cortinarius triumphans*, *Pholiota flammans*, and *Pustularia cupularis* were perhaps the most noteworthy finds among the larger fungi. It was interesting to find again *Naumovia abundans* on *Prunella*, which had been seen in 1931 at Belfast. This fungus was found again on the following day at Gibside, so that it is probably not uncommon in the district. *Corticium coronatum*, a new record for Britain, was identified subsequently.

Unfortunately for us, the much-needed rain arrived in the north on the next day, and at first collecting was considerably hampered by heavy showers. Gibside Park, near Rowlands Gill, Co. Durham, was the place selected, and proved interesting ground, which in a normal season would no doubt be rich in fungi. Actually, however, the bag on this day was far less than at Alnwick. The *Naumovia* already mentioned and *Tulasnella violea* were the only specially noteworthy finds.

In the evening, at 8.30 p.m., the President, Prof. W. Brown, delivered his Presidential Address, entitled "The Mechanism of Disease Resistance in Plants."

On Thursday, September 21st, Dilton Woods near Corbridge were explored. At first a pine wood, with numerous stumps and old fallen

trunks, provided work for those interested in the lower Basidiomycetes. A traverse through some open moorland brought the party to a dense mixed wood with a fair amount of undergrowth. This was, however, not very productive of fungi, and very little of any note was secured.

On the next day, at Chopwell Wood, the ground was even more dry and yielded nothing but a few common species of fungi.

In the evening of Thursday, September 21st, Mr J. Ramsbottom had been invited to deliver a popular lecture at the Hancock Museum. The lecture was on "Edible and Poisonous Fungi" and was well attended. By courtesy of the Council of the Natural History Society of Northumberland the Hancock Museum, one of the oldest in the country, was open free to members of the Society during the week.

The Annual General Meeting was held on Tuesday evening, September 19th, when the Officers and Council for the ensuing year were elected as follows: President, Dr B. Barnes; Vice-Presidents, Prof. W. Brown and Mr Carleton Rea; members of Council to replace three members retiring under the Rules, Mr Cartwright, Mr Bartlett, and Mr Carrothers. The Editors and other Officers remain as before. Mrs Alcock was nominated as delegate to the British Association in 1934.

A cordial invitation from the Norfolk and Norwich Naturalists Society and the Council of the Norwich Museum led to the selection of Norwich as headquarters for the Autumn Foray in 1934. The date was left to the Council to decide in consultation with the Norwich members of the Society.

At the close of the meeting, cordial votes of thanks were passed to the various landowners who had permitted visits to their estates. Special thanks were accorded to the Council of Armstrong College and Prof. Heslop Harrison for hospitality, and particularly to Mr A. W. Bartlett for the trouble taken by him in organising the meeting.

For assistance in compiling the attached list of fungi collected the Secretary is especially indebted to Mr Ramsbottom, Mr Pearson, Mr E. W. Mason, and Mr T. Petch.

*Complete List of Species gathered during the Foray*

*A.* = Hulne Park, Alnwick; *G.* = Gibside Park; *D.* = Dilton Woods; *C.* = Chopwell Wood.

**HYMENOMYCETES**

*Amanita mappa* (Batsch) Fr., *D.*, *C.*, *muscaria* (Linn.) Fr., *A.*, *D.*, *rubescens* (Pers.) Fr., *G.*

*Amanitopsis vaginata* (Bull.) Roze, *A.*, *C.*, *fulva* (Schaeff.) W. G. Sm., *A.*

*Armillaria mellea* (Vahl) Fr., *A.*, *G.*, *C.*, *mucida* (Schrad.) Fr., *A.*

*Lepiota cristata* (A. & S.) Fr., *A.*, *amianthina* (Scop.) Fr., *A.*, *sistrata* Fr., *A.*, *Bucknallii* B. & Br., *A.*

Tricholoma rutilans (Schaeff.) Fr., *A.*, *G.*, *C.*, saponaceum Fr., *A.*, acerbum (Bull.) Fr., *A.*

Clitocybe aurantiaca (Wulf.) Studer, *A.*, *D.*, *C.*, and var. albida (Gill.) Rea, *D.*, cerussata Fr., *G.*, infundibuliformis (Schaeff.) Fr., *G.*, flaccida (Sow.) Fr., *A.*

Laccaria laccata (Scop.) B. & Br., *A.*

Collybia radicata (Reh.) Berk., *A.*, platyphylla (Pers.) Fr., *G.*, fumosa (Pers.) Quél., *G.*, maculata (A. & S.) Fr., *A.*, *D.*, *C.*, tuberosa (Bull.) Fr., *A.*

Mycena pura (Pers.) Fr., *D.*, *C.*, galericulata (Scop.) Fr., *A.*, *C.*, ammoniaca Fr., *A.*, haematopus (Pers.) Fr., *A.*, *G.*, sanguinolenta (A. & S.) Fr., *A.*, galopus (Pers.) Fr., *A.*, rorida Fr., *A.*

Russula chloroides (Krombh.) Bres., *A.*, nigricans (Bull.) Fr., *A.*, adusta (Pers.) Fr., *A.*, lepida Fr., *A.*, cyanoxantha (Schaeff.) Fr., *A.*, *G.*, *D.*, *C.*, foetens (Pers.) Fr., *A.*, ochroleuca (Pers.) Fr., *A.*, *G.*, *C.*, fellea Fr., *A.*, drimeia Cooke var. Queletii (Fr.) Bat., *A.*, *D.*, fragilis (Pers.) Fr., *A.*, *G.*, and var. fallax (Schaeff.) Mass., *D.*, *C.*, emetica (Schaeff.) Fr., *A.*, atropurpurea (Krombh.) Maire, *G.*, xerampelina (Schaeff.) Fr., *A.*, puellaris Fr., *A.*, vesca Fr., *G.*

Lactarius torminosus (Schaeff.) Fr., *A.*, turpis (Weinm.) Fr., *D.*, blennius Fr., *A.*, uvidus Fr., *A.*, pyrogalus (Bull.) Fr., *A.*, chrysorheus Fr., *A.*, vellereus Fr., *A.*, deliciosus (Linn.) Fr., *A.*, quietus Fr., *A.*, *D.*, rufus (Scop.) Fr., *D.*, glycosmus Fr., *A.*, serifluus (DC.) Fr., *A.*, mitissimus Fr., *A.*, subdulcis (Pers.) Fr., *A.*

Pleurotus sapidus Schulz., *G.*

Cantharellus cibarius Fr., *D.*

Marasmius peronatus (Bolt.) Fr., *G.*, *C.*, esculentus (Wulf.) Karst., *A.*, *D.*, hariorum (DC.) Quél., *A.*, *G.*, *C.*, impudicus Fr., *D.*, dryophilus (Bull.) Karst., *A.*, *D.*, ramealis (Bull.) Fr., *D.*, *C.*

Androsaceus androsaceus (Linn.) Pat., *D.*

Lentinus cochleatus (Pers.) Fr., *A.*

Pluteus cervinus (Schaeff.) Fr., *G.*, salicinus (Pers.) Fr., *G.*

Entoloma nidorosum Fr., *A.*

Nolanea cetrata (Fr.) Schroet., *A.*, *D.*

Clitopilus prunulus (Scop.) Fr., *A.*

Paxillus involutus (Batsch) Fr., *A.*, *D.*

Pholiota squarrosa (Mull.) Fr., *A.*, spectabilis Fr., *A.*, *D.*, flammans Fr., *A.*, mutabilis (Schaeff.) Fr., *A.*, *G.*

Inocybe geophylla (Sow.) Fr., *A.*, and var. lilacina Fr., *A.*, obscura (Pers.) Fr., *A.*, perlata Cooke, *A.*

Astrosporina calospora (Quél.) Rea, *A.*

Hebeloma crustuliniforme (Bull.) Fr., *A.*, subsaponaceum Karst., *A.*

Galera hypnorum (Schrank) Fr., *A.*, tenera (Schaeff.) Fr., *A.*

Naucoria escharoides Fr., *A.*

Flammula sapinea Fr., *D.*, ochrochlora Fr., *D.*

Corticarius (Phlegmacium) triumphans Fr., *A.*, (Myxacium) elatior Fr., *G.*, *C.*, (Telamonia) rigidus (Scop.) Fr., *A.*, *G.*, (Hydrocybe) leucopus (Bull.) Fr., *A.*, acutus (Pers.) Fr., *A.*

Crepidotus mollis (Schaeff.) Fr., *A.*

Psalliota sylvatica (Schaeff.) Fr., *A.*

Stropharia aeruginosa (Curt.) Fr., *A.*

Hypholoma sublateritium (Schaeff.) Fr., *A.*, *C.*, fasciculare (Huds.) Fr., *A.*, *D.*, *C.*, hydrophilum (Bull.) Fr., *D.*

Psilocybe uda (Pers.) Fr., *D.*, semilanceata Fr., *G.*, *C.*

Psathyrella disseminata (Pers.) Fr., *A.*, atomata Fr., *D.*

Anellaria separata (Linn.) Karst., *G.*

Coprinus comatus (Fl. Dan.) Fr., *A.*, atramentarius (Bull.) Fr., *A.*, *G.*, micaceus (Bull.) Fr., *A.*, lagopus Fr., *A.*

Boletus luteus (Linn.) Fr., *D.*, elegans (Schum.) Fr., *A.*, viscidus (Linn.) Fr., *A.*, granulatus (Linn.) Fr., *A.*, badius Fr., *A.*, *D.*, variegatus (Sow.) Fr., *D.*, chrysenteron (Bull.) Fr., *A.*, *G.*, subtomentosus (Linn.) Fr., *D.*, *C.*, pruinatus Fr., *A.*, edulis (Bull.) Fr., *A.*, scaber (Bull.) Fr., *A.*

*Polyporus nummularius* (Bull.) Quél., *squamulosus* (Huds.) Fr., *A.*, *G.*, *sulphureus* (Bull.) Fr., *A.*, *G.*, *giganteus* (Pers.) Fr., *A.*, *G.*, *betulinus* (Bull.) Fr., *A.*, *G.*, *D.*, *C.*, *adiposus* B. & Br., *G.*, *caesius* (Schrad.) Fr., *A.*, *trabeus* Fr., *A.*  
*Fomes annosus* Fr., *A.*  
*Ganoderma applanatum* (Pers.) Pat., *A.*  
*Poria sanguinolenta* (A. & S.) Fr., *A.*, *hymenocystis* B. & Br., *A.*, *D.*  
*Polystictus versicolor* (Linn.) Fr., *A.*, *G.*, *abietinus* (Dicks.) Fr., *D.*  
*Irpea obliquus* (Schrad.) Fr., *D.*  
*Fistulina hepatica* (Huds.) Fr., *A.*  
*Hydnnum repandum* (Linn.) Fr., *A.*  
*Grandinia farinacea* (Pers.) Bourd. & Galz., *A.*, *G.*, *granulosa* Fr., *A.*  
*Hypochnus fuscus* (Pers.) Fr., *A.*, *fumosus* Fr., *D.*, *phylacteris* (Bull.) Rea, *A.*  
*Stereum spadiceum* Fr., *A.*, *G.*, *D.*, *rugosum* Fr., *A.*, *G.*, *hirsutum* (Willd.) Fr., *A.*, *G.*  
*Corticium Sambuci* (Pers.) Fr., *trigonospermum* Bres., *A.*, *coronatum* (Schroet.) v. Hoehn. & Litsch., *A.*, *botryosum* Bres., *A.*, *subcoronatum* v. Hoehn. & Litsch., *A.*, confine Bourd. & Galz., *G.*, *porosum* B. & C., *A.*  
*Corticium polygonum* (Pers.) Fr., *C.*, *praetermissum* (Karst.) Bres., *A.*, *albostramineum* (Bres.) Bourd. & Galz., *A.*  
*Peniophora byssoides* (Pers.) v. Hoehn. & Litsch., *A.*, *G.*, *velutina* (DC.) Cooke, *A.*, *setigera* (Fr.) Bres., *A.*, *hydnoides* Cooke & Mass., *A.*, *quercina* (Pers.) Cooke, *G.*, *C.*  
*Clavaria cristata* (Holmsk.) Fr., *A.*  
*Platygloea effusa* Schroet., *A.*  
*Exidia glandulosa* (Bull.) Fr., *D.*  
*Tulasnella violea* (Quél.) Bourd. & Galz., *G.*  
*Dacryomyces deliquescens* (Bull.) Duby, *G.*, *D.*, *C.*  
*Calocera viscosa* (Pers.) Fr., *D.*, *cornea* (Batsch) Fr., *G.*

### GASTEROMYCETES

*Phallus impudicus* (Linn.) Pers., *G.*  
*Lycoperdon giganteum* (Batsch) Pers., *A.*, *pyriforme* (Schaeff.) Pers., *A.*, *G.*  
*Scleroderma aurantium* Pers., *A.*, *verrucosum* (Vaill.) Pers., *A.*

### UREDINALES

*Uromyces Alchemillae* (Pers.) Lév., *A.*  
*Puccinia Violae* (Schum.) DC., *A.*, *G.*, *aegra* Grove, *A.*, *Lychnidearum* Link, *A.*, *pulverulenta* Grev., *A.*, *Epilobii* DC., *C.*, *Chrysosplenii* Grev., *G.*, *Chaerophylli* Purt. on *Myrrhis odorata*, *G.*, *obtegens* (Link) Tul., *A.*, *Crepidis* Schroet., *C.*, *Hieracii* (Schum.) Mart., *C.*, *Chondrillae* Corda on *Lactuca muralis*, *C.*, *Senecionis* Lib., *A.*, *Primulæ* (DC.) Duby, *A.*, *Veronicae* Schroet. on *Veronica montana*, *A.*, *Glechomatis* DC., *A.*, *Menthae* Pers., *A.*, *annularis* (Str.) Schlecht., *A.*, *Acetosae* (Schum.) Koern., *A.*, *Buxi* DC., *A.*, *obscura* Schroet., *A.*, *D.*, *Poarum* Niels. (Aecidium on *Tussilago*), *A.*, *C.*, *mirabilissima* Peck, *A.*  
*Triphragmium Ulmariae* (Schum.) Link, *A.*  
*Phragmidium mucronatum* Schlecht., *A.*, *violaceum* (Schultz) Wint., *A.*  
*Coleosporium Tussilaginis* (Pers.) Kleb., *A.*  
*Pucciniastrum Circaeae* (Schum.) Schroet., *A.*, *G.*, *Epilobii* (Pers.) Otth, *A.*  
*Milesina Blechni* Syd., *D.*  
*Melampsoridium betulinum* (Pers.) Kleb., *A.*, *D.*, *C.*

### USTILAGINALES

*Ustilago violacea* (Pers.) Wint., *A.*  
*Entyloma Calendulae* (Oud.) de Bary, *A.*  
*Urocystis Anemones* (Pers.) Schroet. on *Ranunculus repens*, *A.*, *G.*

## PLECTASCALES

*Elaphomyces granulatus* Fr., *D.*  
*Ctenomyces serratus* Eidam, *A.*

## PYRENOMYCETES

*Sphaerotheca pannosa* (Wallr.) Lév., *A.*  
*Podosphaera Oxyacanthae* (DC.) de Bary, on *Vaccinium Myrtillus*, *D.*  
*Erysiphe Polygoni* DC. on *Hypericum*, *A.*, *cichoriacearum* DC. on *Senecio*, *A.*  
*Uncinula Aceris* (DC.) Sacc., *A.*  
*Nectria cinnabarina* (Tode) Fr., *G.*, *C.*  
*Claviceps purpurea* (Fr.) Tul., *G.*, *microcephala* (Wallr.) Tul., *D.*  
*Stigmata Robertiani* Fr., *G.*  
*Naumovia abundans* Dobr. on *Prunella*, *A.*, *G.*  
*Bertia moriformis* (Tode) de Not., *A.*  
*Sphaerulina Taxi* (Cooke) Mass., *A.*  
*Diatrypella quercina* (Pers.) Nits., *A.*  
*Diatrype Stigma* (Hoffm.) Fr., *A.*, *disciformis* (Hoffm.) Fr., *G.*  
*Ustulina vulgaris* Tul., *A.*  
*Xylaria Hypoxylon* (Linn.) Grev., *A.*, *polymorpha* (Pers.) Grev., *A.*, *carpophila* (Pers.) Fr., *A.*  
*Phyllachora graminis* (Pers.) Fuck., *A.*, *C.*  
*Endodothella Junci* (Fr.) Theiss. & Syd., *D.*  
*Dothidella betulina* (Fr.) Sacc., *A.*

## HYSTERICIALES

*Lophodermium Pinastri* Chev., *D.*

## DISCOMYCETES

*Galactinia badia* (Pers.) Boud., *D.*  
*Pustularia cupularis* (Linn.) Fuck., *A.*  
*Lachnea hemisphaerica* (Wigg.) Gill., *A.*  
*Taphrina Tosquinetii* (West.) P. Magn., *A.*  
*Helotium fructigenum* (Bull.) Fuck., *A.*  
*Orbilia xanthostigma* Fr., *A.*  
*Sclerotinia Curreyana* (Berk.) Karst., *A.*  
*Dasyscypha virginea* (Batsch) Fuck., *G.*  
*Trichoscypha calycina* (Schum.) Boud., *D.*, *C.*  
*Mollisia cinerea* (Batsch) Karst., *A.*  
*Fabraea Ranunculi* (Fr.) Karst., *A.*  
*Stegia Illicis* Fr., *A.*, *G.*  
*Rhytisma acerinum* (Pers.) Fr., *A.*, *G.*, *C.*

## PHYCOMYCETES

*Syzygites megalocarpus* Ehrenb. on *Lycoperdon giganteum*, *A.*  
*Plasmopara nivea* Schroet., *G.*  
*Entomophthora aphrophorae* Rostr. on froghoppers, *D.*

## DEUTEROMYCETES

*Actinonema Rosae* (Lib.) Fr., *A.*  
*Oidium alphitoides* Griff. & Maubl., *D.*, *C.*  
*Botrytis cinerea* Pers. on *Scilla*, *A.*  
*Rhinotrichum repens* Preuss, *A.*, *Thwaitesii* B. & Br., *A.*  
*Sepedonium chrysospermum* (Bull.) Fr., *D.*  
*Cephalosporium muscarium* Petch, on fly, *C.*

*Ovularia obliqua* (Cooke) Oud., *A.*, *G.*, *C.*, *primulana* Karst., *A.*  
*Ramularia Primulae* Thuem., *A.*, *calcea* (Desm.) Ces., *A.*, *sambucina* Sacc., *A.*,  
    *Ajugae* Niessl., *A.*, *acris* Lindr., *A.*, *Urticae* Ces., *A.*, *Taraxaci* Karst., *A.*,  
    *Cirsii* Allesch., *A.*  
*Fusicladium depressum* (B. & Br.) Sacc., *C.*  
*Cladosporium herbarum* (Pers.) Link, on dead flies, *C.*  
*Cercospora Mercurialis* Pass., *A.*, *C.*  
*Sporocybe Azaleae* Peck, *A.*  
*Stilbella erythrocephala* (Ditm.) Lindau, *A.*  
*Isaria farinosa* (Holmsk.) Fr., *C.*, *sphecophila* Ditm. on an ichneumon, *C.*  
*Hymenostilbe arachnophila* (Ditm.) Petch, on spiders, *D.*, *C.*

MYCETOZOA FOUND DURING THE FORAY OF  
THE BRITISH MYCOLOGICAL SOCIETY AT  
NEWCASTLE, SEPTEMBER 18TH-21ST, 1933

BY G. LISTER

AFTER the drought of the summer months it was not surprising that our harvest of Mycetozoa was not large. The total list of species found was twenty-two, one of which, however, *Cibraria macrocarpa*, had not been recorded before from England, and only twice from Scotland. On September 19th the Hulne Abbey Woods were visited, where fine groves of ash, sycamore, oak and Douglas Spruce clothed the steep banks of a stream; eleven species of Mycetozoa were found. On September 20th, Gibside Park should have given very good hunting, but heavy rain proved impeding. On September 21st we were conveyed to Dilton Moor, where the woods of Scotch Fir, with undisturbed fallen branches, provided many colonies of species usually associated with coniferous wood. It was here that *Cibraria macrocarpa* was found on dead branches, in a rather mouldy condition; *C. rufa* was abundant. Yellow plasmodium, creeping in a thick bed of pine-needles, was brought away and kept moist; after five weeks it developed typical sporangia of *Leocarpus fragilis*.

In the following list *H.*, *G.* and *D.* refer to gatherings from Hulne Abbey Woods, Gibside and Dilton Woods respectively.

*Ceratiomyxa fruticulosa* (Mueller) Macbr., *D.*  
*Physarum nutans* Pers. and var. *leucophaeum* Lister, *H.*  
*Fuligo septica* (L.) Gmel., *H.*  
*Leocarpus fragilis* (Dicks.) Rost., *D.*  
*Didymium difforme* (Pers.) Duby, *H.*  
*Stemonitis fusca* Roth, *H.*  
*S. flavogenita* Jahn, *H.*  
*Comatricha nigra* (Pers.) Schroeter, and var. *alta* Lister, *D.*  
*C. typhoides* (Bull.) Rost., *H.*  
*Cibraria argillacea* Pers., *G.*  
*C. rufa* (Roth.) Rost., *D.*  
*C. macrocarpa* Schrader, *D.*  
*Dictyium cancellatum* (Batsch) Macbr. var. *fuscum*, *D.*  
*Tubifera ferruginosa* Gmel., *D.*  
*Lycogala epidendrum* (L.) Fries, *D.*  
*Trichia verrucosa* Berk., *D.*  
*T. affinis* de Bary, *H.*  
*T. decipiens* (Pers.) Macbr., *H.*  
*T. Botrytis* Pers., *G.*, *D.*  
*Arcyria cinerea* (Bull.) Pers., *H.*, *G.*, *D.*  
*A. denudata* (L.) Wetst., *H.*  
*A. incarnata* Pers., *H.*

## PRESIDENTIAL ADDRESS

By W. BROWN, M.A., D.Sc.

### MECHANISM OF DISEASE RESISTANCE IN PLANTS

THE subject of disease resistance in plants, considered from the point of view either of academic or practical interest, is of too wide a scope to allow of adequate treatment in such an address as I propose to give. Relevant material could probably be culled from almost any paper dealing with a plant pathological subject. There is the variation of susceptibility from one plant or variety to another and the different behaviour of the same plant under different environmental conditions. Viewed from another standpoint, there are such matters of interest as the pathogenic range of various fungal parasites and the differences in virulence shown by strains, biological races, etc., of the same fungal species. Data of this type would all contribute to make up the full story of disease resistance, but it is doubtful if any summary, covering the whole field, could be usefully attempted on this occasion. For those of you who might wish to read more generally on the subject, a number of papers might be cited, e.g. by Marshall Ward and Appel among earlier writers and more recently by Brooks and Walker. To the last mentioned I would specially refer you for a good and comprehensive catalogue of the types of relationship shown in parasitism.

I propose therefore to restrict the scope of my remarks to physiological aspects of parasitism, and it is for this reason that I have introduced the word "mechanism" into the title. Parasitism will be considered merely from chemical and physical points of view, and obviously one can deal only with those types of parasitism which have so far proved to be amenable, in some degree, to physiological analysis. This in itself is a very considerable restriction, and I shall now proceed to indicate more specifically certain parts of the subject which, though they may possess very great interest or importance in other respects, do not call for treatment here.

The obligate type of parasite, of which perhaps the most familiar example is *Puccinia graminis*, has always been looked upon as possessing special interest, and rightly so. The parasite-host relationship may be strikingly different with strains of the parasite which are scarcely distinguishable in any morphological respect, or again the same fungal strain may show very different effects on certain varieties of the host plant. The facts are well known to botanical readers and need only be summarised briefly.

In one case, where the strain of the fungus is brought into contact

with the right variety of host plant, the former proceeds, under suitable conditions, to send haustoria into the cells of the latter and to establish what is called a symbiotic relationship, at least for some time. That is, both the parasite and the invaded part of the host continue to thrive. There may even be, and often is, a stimulation of the host tissue showing itself in a more vigorous metabolism, as exemplified by a greater richness of contents than in the normal unininvaded cells or by a restarting of growth. The invaded cell and perhaps also unininvaded cells in the neighbourhood may enlarge abnormally or may even begin to divide. In this way arise the galls which are more or less characteristic of this type of parasitic relationship.

A very different sequence of events may be shown when a specialised parasite attacks a variety of the host which is somewhat resistant. Up to a point the process of invasion is the same as in the preceding, but from about the time when haustoria are pushed into the host cells differences arise. The haustoria are typically fewer in number and, so far as one can judge from microscopical appearance, do not seem to function vigorously. More interesting, however, is the reaction of the host tissue. The invaded cells and others nearby are soon killed, with the result that the parasite becomes hedged round by a zone of dead host tissue. As it so happens that this type of parasite can grow only on cells which are actually alive, no further progress is possible. Thus arises the curious position that the resistance to attack of the plant as a whole is based on high susceptibility ("hypersensitiveness") of its individual cells to the action of the parasite, as is shown by their being rapidly killed when invaded.

A third type of relationship has been described in which a specialised parasite is brought into contact with a plant widely removed botanically from its normal host. In such a case, the hyphae of the parasite may freely enter the intercellular spaces of the plant but they do not succeed in forming haustoria. At some stage or other the invading hyphae are killed, possibly by the action of some toxic exudation from the host cells which on their part remain unaffected.

Any attempt to study the physiology of the type of parasite which has just been described comes up against the difficulty that the highly specialised parasite cannot, so far as is known, be cultivated on any artificial medium. A decoction even of the plant which it parasitises vigorously is no more suitable for the purpose than is plain water or any other medium. A study of the metabolism of such a fungus is thus extremely difficult inasmuch as the only known substrate—the living plant—is highly complex. With fungi which are amenable to cultural treatment, one can at least begin operations with a medium of known and relatively simple composition, and however complex the changes brought about by the fungus, results are obtainable up

to the limits set by chemical technique. On the basis of these results one can attempt to interpret the behaviour of the fungus in its capacity of parasite. For the reasons stated, this line of deduction cannot even be begun with such a parasite as *Puccinia graminis*, so that we are limited to such information as is obtainable by cytological study. While the appearances presented are undoubtedly interesting, it is more than doubtful if the cytological method can ever lead to an understanding of the physiological processes involved. Interpretations in physiological terms can be and have been put forward, but these are nothing more than guesses supported by analogy with better known instances. One may plausibly postulate toxins or enzymes to explain one effect or another, but no direct evidence for the existence of these has yet been produced. Again, with reference to the marked specialisation of parasitism shown, it has been suggested that nutritive selection of particular isomeric forms of starch or protein is the underlying factor, but this is mere speculation. At the moment therefore the physiology of the specialised parasite is practically unknown, nor does there seem to be much hope of progress in that direction until someone discovers just why artificial media are useless for the growth of that type of fungus. Presumably the elusive substance is some intermediate and labile product of carbon—or nitrogen—assimilation, so that the clue should be and be provided by the plant physiologist. It is clear therefore that the highly specialised or obligate parasite may be largely left aside so far as the present discussion is concerned.

To go now to the other end of the scale, there is a whole group of effects which are more correctly described under the heading of "disease escape" than of real resistance. Certain plants or plant varieties do not in practice suffer from such and such a disease though in reality they may be just as susceptible as others which do suffer. The point is that either from some cultural practice or from something in the habit of the plant which makes it difficult for the parasite to come into effective contact with the host, the conditions are rendered unsuitable for attack. A few of the familiar illustrations may be cited. Early potatoes may be as susceptible to blight as many of the main-crop varieties; yet blight is not in general a problem where the former are concerned, as they are removed from the land before the blight organism is normally prevalent. Again both cos and cabbage types of lettuce are susceptible to attack by the grey-mould fungus, *Botrytis cinerea*, and both may in fact be destroyed in the seedling stage over the winter or in early spring. During a normal summer however the damage to cos types is negligible whereas cabbage types may from time to time be seriously affected. This difference in response is undoubtedly correlated with the different growth habits of the two types, the large spreading leaves of a cabbage

lettuce, which are closely appressed to the ground, forming a kind of natural moist chamber which is very favourable to germination of the fungal spores with subsequent attack at the collar region. Similarly the presence of bloom on various grasses, of hairs, etc., may prevent the wetting of a plant surface after rain and thus remove one of the factors which is necessary for the initiation of attack. Features of such a kind, though they may be of great practical value, and though the mechanism concerned may be quite well understood, are not relevant to any discussion of real resistance.

A third aspect of resistance, viz. its genetical behaviour, is of very great theoretical and practical importance and has led to an enormous amount of detailed experimental work. Diseases due to specialised and non-specialised parasites have been studied from this point of view, but in general the data are not of the kind which can be interpreted in physiological terms. This very extensive field of study must therefore also be omitted here.

I now come to my subject proper. Assuming that all three factors which lead to disease are present—viz. fungus + plant + suitable environmental conditions—what means does the fungus adopt to enter (and parasitise) the plant, and conversely by what means does the plant attempt to prevent it from doing so? I shall attempt to dissect the process of successful attack into a series of stages which will be dealt with one by one. As I have been concerned for some years in research upon these matters, I shall endeavour not merely to state what views have been held or are now held on the various topics but to indicate as far as possible where further work is called for and more especially where it is feasible to make advances with the technique available at the moment. In other words I shall examine the subject as a field for further research.

#### MECHANISM OF PENETRATION

The first point that arises is—does the plant exercise any inducement to the fungus to enter or is entrance merely accidental? The question of a possible directive influence, due to chemical substances, upon the movement of motile cells was first taken up by Pfeffer some fifty years ago and later studied by his student, Miyoshi, with special reference to the growth of fungal germ tubes. The latter worker makes out what appears to be a complete case for a directive chemical stimulation ("Chemotropism"). Germ tubes are described as passing through minute openings in artificial films or through permeable membranes or into glass capillaries, the attractive agent in each case being the appropriate concentration of some chemical placed on the opposite side of the membrane or in the capillary tube. Unfortunately Miyoshi's work is largely refuted, in matters of fact, by researches carried out later by a number of investigators, e.g. Clark and Fulton,

who failed to find much evidence for the positive chemotropism of Miyoshi, but substituted instead a negative chemotropism or growth away from certain products made by the fungus itself. The latest detailed work on the subject, by Graves, found some truth in both the earlier views, viz. that both types of tropism can be demonstrated but that the negative tropism to fungal metabolic products is the greater effect. It is in fact abundantly clear, even from internal evidence, that some of Miyoshi's conclusions are highly overdrawn. Graves's paper is the latest of any importance on chemotropism of fungal hyphae, and, though the subject cannot be considered as adequately worked out yet, we must accept his conclusions as the best available for the time being.

When we come to consider how far the phenomenon of chemotropism plays a part in the initiation of parasitism, we find considerable divergence in the views expressed. Massee in an early paper accepted Miyoshi's results in their entirety and proceeded to construct a physiology of fungal attack on this basis. According to his view, when chemotropic substances diffuse out of the host tissue on to the surface, fungi enter; when there is no such diffusion, there is no entry. Specialised parasites are those which respond to a special substance, and a non-specialised parasite responds to nutrients in general. Now there is no doubt that such an interpretation is very wide of the mark, and it is sufficient to point out, as was pointed out long ago, that fungi will often enter a host which they are quite unable to parasitise. Penetration is merely one of a number of steps which lead to parasitism.

By other writers the chemotropic theory has been applied with greater reserve to the explanation of parasitism. Fulton suggests that under conditions of a drying atmosphere, the germ tubes of fungi may be attracted by the turgid cells underlying the stomata ("hydrotropism"). The negative tropism of hyphae to each other may, according to Graves, be responsible for the ramification of the fungus through the host tissue. In plant pathological papers generally, chemotropism is usually assumed or suggested as a factor in fungal growth, without the production of any fresh evidence bearing on the point.

In examining the applicability of these theories of chemotropism to the initiation of parasitism, it will be well to distinguish the two modes of entry available, cuticular and stomatal. With regard to the former, it is quite plausible that a fungal germ tube growing over the surface of the plant might be unequally stimulated on its near and far sides by some chemical diffusing out of the underlying cells. In response to this unilateral effect, it might be induced to grow towards the source of the stimulating substance. On the other hand, experiments have shown quite definitely that penetration of artificial

or natural membranes by the germ tubes of *Botrytis cinerea* readily takes place no matter what the original distribution of the nutrient substances might be, *i.e.* the fungus penetrates equally well with or against the gradient of chemotropic substance, or if there is no gradient at all. Miyoshi's and Massee's observations, that penetration of certain plants did not occur when the underlying tissue was injected with water but that it did so when a sugar solution was used, can be explained on grounds other than chemotropism, as will be shown later. It is clear therefore that chemotropism to stimulatory substances is not a necessary factor for cuticular penetration, though it has not been disproved—and it would require a very careful quantitative examination to disprove it—as a contributing factor in the process.

The application of Fulton's negative tropism to the explanation of cuticular penetration is a physical impossibility. At first glance it might seem that the accumulation of staling products in the infection drop would cause the germ tubes to turn away from the region of high concentration—viz. the infection drop—to a region of no concentration, viz. the underlying host cells. This, however, is begging the question. The response of the germ tubes can be determined only by conditions within the infection drop, and there is no reason why there should be a lower concentration of staling substance on the side next the cuticle than on the side away from it. In fact, on principles of diffusion, the reverse is more likely, and one would expect the hyphae, if subject to this negative tropism, to turn away from the cuticle.

As regards stomatal penetration, very little of the work of Miyoshi, Fulton, or Graves appears to be relevant. The perforated mica plate, which has been used so much in researches on chemotropism, is presumed to furnish a working model of the plant epidermis with its stomata. An important difference however is that the substomatal chamber is normally full of air, so that there is no means for the outward diffusion of sugars, salts, etc., which are the presumed chemotropically active substances. If there is any chemotropic influence concerned, it must arise from some volatile substance. Balls has in fact suggested that the germ tubes of rust spores pass through the stomata of the host plant as the result of a positive tropism to water vapour.

Chemotropic theories being thus unsatisfactory, one has recourse to the alternative view, which has also been suggested from time to time, viz. that the stimulus to penetration is a contact one, at least as regards entry through the cuticle. The theory of contact-tropism has the great disadvantage that it is very difficult to explore experimentally, and in the main it is rather based on a negative, *i.e.* the inadequacy of the chemotropic theories. There is, however, some definite evidence in its favour. Thus a germ tube of *Botrytis cinerea*,

when on the point of penetrating the cuticle of a plant, produces a slight swelling or "appressorium" whereby, through partial gelatinisation of the fungal wall, the tip of the hypha is firmly attached to the surface of the host. From this appressorium the penetrating hypha is put out through the cuticle in the form of a fine peg or thread. Now when a germ tube of the same fungus is grown on a glass slide, a whole series of such appressoria may be formed. There is of course no penetration, but it is reasonable to suppose that each appressorium represents an attempt to penetrate, that after a time the fungus resumes growth but soon tries again, and so on. There can be no question of a chemotropism in such a case.

The adoption of a theory of contact-tropism in preference to a chemical one does not mean that chemical factors are of no importance in connection with the stimulus to penetrate. Any particular fungus may react differently according to the medium in which it is growing, *i.e.* chemical factors may decide whether appressoria are or are not formed in response to a contact stimulus. In the absence of any definite information on this point and on the further point as to whether response to contact is in any way influenced by the physical nature of the surface touched, the question of tropisms may be left with the statement that so far the theory of contact-tropism is the only one to which damaging objections cannot for the present be raised.

As regards entry through the cuticle, the further point now arises as to the mechanism of the actual process of penetration. Here again two theories, a mechanical and a chemical, hold the field. According to the latter some substance is excreted by the fungus which softens or dissolves the cuticle. The difficulty is that no one has demonstrated the existence of such a chemical substance. The enzyme pectinase which is secreted by many fungi and which actively dissolves certain cell wall constituents is, so far as is known, quite inert when brought into contact with a cuticularised surface. It is just the outermost layer which is unaffected, but this is all-important. There may also be occasional plant parts which are not sufficiently protected, but the rule is overwhelmingly as already stated. Some evidence in favour of a chemical agent has been adduced from cytological studies, *e.g.* from the appearance of some kind of staining reaction below the cuticle in the neighbourhood of a penetrating hypha, and at a time when penetration has not yet been effected. Apart from the very considerable risk of misinterpreting the exact sequence of events—for the earliest phase of penetration is very difficult to fix properly—there is the criticism that any such staining reaction is not evidence bearing on the question of softening or dissolving of the cuticle.

One has therefore, as before, to fall back upon a theory of mechanical penetration. While it is impossible to outline the mechanics

of the process, a considerable amount of evidence can be adduced in favour of this view. Thus it has been shown that fungi are able to penetrate a variety of membranes—e.g. collodion, paraffin wax, gold leaf—which in all probability they are unable to attack by chemical means. My own experiments with membranes of formalised gelatine of graded hardness can only be interpreted on the mechanical theory. Brown and Harvey's work on the penetration of *Eucharis* leaf by *Botrytis cinerea* showed that the mechanical resistance to penetration of an epidermis is conditioned in part by the hydrostatic backing of the cells behind, and again the results were strongly in favour of the view that the mechanism of penetration is physical.

The *a priori* objection, that it is incredible that such a soft thing as a fungal germ tube can penetrate such a hard thing as a plant cuticle, has no justification in fact and is fully met by a recital of the types of membrane which fungi have been shown to penetrate. The germ tube, it may be remembered, does not penetrate as such but in the form of an extremely fine peg, which may subsequently enlarge to more or less normal diameter when the mechanical strength of epidermis + cuticle has been largely destroyed by enzymic digestion from within, *i.e.* after the enzymically impermeable cuticular barrier has been passed.

Quite a number of observers have supported the mechanical theory of penetration from careful microscopic work, but of course it is not impossible that some fungi may have some chemical means of carrying out or perhaps assisting in the process. Up to the present however no satisfactory evidence of the existence of a cuticle-dissolving enzyme is forthcoming.

The mechanical theory of penetration in its simplest form would entail the possibility that parasitic fungi could be arranged in a series as regards power of penetration and conversely that host epidermes could be similarly graded according to their intrinsic mechanical resistance. It has in fact been shown, by the use of membranes of graded hardness, that *Botrytis cinerea* has a greater capacity to penetrate than has *Penicillium glaucum* which again is more active in that respect than *Rhizopus nigricans*. This series is in agreement with the parasitic tendencies of the three fungi. Further research however may show that the matter is not so simple and that such a state of affairs as is indicated in the following scheme may exist:

	Host A	Host B
Fungus <i>a</i>	+	-
Fungus <i>b</i>	-	+

where + indicates penetration (not necessarily leading to macroscopically visible parasitism). If such a relationship were established the simple mechanical theory would require modification.

Successful penetration means that a chain of effects has been completed. First of all the fungus has been stimulated to attach itself to the host surface, and then to attempt to send in a process at some point of the area of contact. Finally there is the physical act of penetration. Whether the stimulus which produces attachment is the same as that which leads to penetration is not known. From these considerations, it is clear that the theory of mechanical penetration is sufficiently elastic to allow of the process being selective, as envisaged in the scheme above. The nutritional relationships, to be discussed in the following paragraphs, would also need to be borne in mind. A critical study of the whole process is unfortunately still lacking.

A discussion of the mechanism of penetration is incomplete without some consideration of the sources of energy available to the fungus whereby it is able to reach the underlying host tissue. The spores must germinate with sufficient vigour and speed to enable entry to take place while favourable environmental conditions (presence of dew, rain, etc.) prevail. Three possibilities come up for consideration here.

1. The spore itself may contain the necessary food reserves. Germination studies in distilled water show that there is considerable variation among fungi with regard to the capacity of the spores to germinate on their own resources. Again, spores of the same fungus respond very differently according to age or to the manner in which the fungus has been grown. Thus, in a general way, young spores germinate quickly and evenly, with stout germ tubes, and to a high percentage. As they become older ("attenuated by age"), the percentage germination diminishes, so that a sample field shows some spores with fairly long thin germ tubes and others which do not germinate at all. Spores of this type may still be able to germinate vigorously and fairly evenly if supplied with a trace of food. It is obvious that spores are capable of greater parasitic activity at their period of optimal germination than at other times.

Frequently however the fungus, whether as spore or as mycelium, which is in contact with the surface of the host plant, has access to extraneous food supplies, and that in a purely passive manner. Soil fungi have the benefit of food substances present in the soil solution. Even on subaerial parts, where the fungus is in contact with initially pure water such as dew, it does not follow that that water remains pure throughout. It can be shown very simply that appreciable exosmosis takes place from many living plant tissues, through the cuticle, into drops of water laid on the surface, and that this process goes on independently of any fungal spores which may be present in the water. The effect of this exosmosis is in many cases to increase the vigour of spore germination; in others there is a repression or

even inhibition. Though the amount of chemical substance so rendered available to the fungus may actually be very small, it is enough to affect markedly the vigour of germination.

The third possibility rests on the statement of de Bary, in his pioneer researches on *Sclerotinia*, that certain parasites are able to kill underlying cells of the host before penetration has actually been effected, and by that means to have access to soluble food substances which diffuse out from the killed cells. De Bary is responsible for the view that parasites of the facultative type invade only after previous saprophytic feeding. The hypothesis of "killing in advance of penetration" is a corollary to the general view. Neither of these has been fully borne out by later work. The necessity for saprophytic nourishment as a preliminary to parasitism is definitely an overstatement. It is more correct to say that with spores of low inherent vigour, saprophytic nourishment materially enhances the ability to parasitise. The claim that certain parasites kill in advance of penetration has also not been substantiated by more recent critical studies. The subject is one of considerable technical difficulty, even with modern cytological methods, and it is not surprising that de Bary somewhat misinterpreted the sequence of events. From his own writings it is evident that de Bary was not satisfied with his conclusions, and the acceptance of the latter by other workers (e.g. Nordhausen) led to some irreconcilable results. It is obvious that the theory of killing in advance of penetration requires the excretion by parasitic fungi of some toxic substance which is capable of diffusing through the plant cuticle. This subject will be discussed later in a somewhat different connection; in the meanwhile it is sufficient to state that no satisfactory evidence of the existence of such a substance has been advanced. Until such time as the necessary evidence is forthcoming, the theory under consideration may be discarded.

The protection afforded to a plant by its outer layer (cuticle or bark) is undoubtedly of very great importance. Many plants are immune to attack from certain fungi only so long as the surface is intact. In such a case the fungus is spoken of as a "wound parasite." The susceptibility of some young structures (young leaves, meristematic regions) to attack while the older mature parts are resistant has similarly been ascribed to the strengthening of the cuticle as maturity increases. Familiar examples are seen in the incidence of apple rust and apple scab. The greater resistance of mature plants of cereals as compared with that of seedlings to attack by the uredospores of *Puccinia graminis* is not relevant in this connection since penetration is through the stomata. Some question of internal resistance is therefore concerned, and as regards the two apple diseases cited, it might be added that, though the mode of penetration is cuticular, internal factors of resistance may likewise be operative.

## INTERNAL RESISTANCE

Perhaps undue attention has been paid to penetration as this is not, after all, the most important or the most interesting phase in the establishment of parasitism. As has been already stated, fungi may often enter within the tissue of a plant without attack ensuing. One may therefore put such questions as the following. Why is it that, if any parasite is put into any plant at random, *i.e.* all questions of penetration being side-tracked by placing the potential parasite into a wound, attack does not develop? Why is a so-called saprophytic fungus unable to parasitise? Or, to take a more particular example, why is a parasitic fungus able to attack under one set of conditions and not under others? These questions obviously cover a wide ground, and make up in fact the fundamental problem of plant pathology.

As has already been noted, the only rational method of constructing a physiology of parasitism is to study the growth activities of fungi on media of known composition and to attempt to apply the results to the more complex case where the fungus is growing on a living plant. Before turning to a consideration of the main features of fungal metabolism so far as they may be reckoned to bear on parasitism, it will be well to point out what is the essential difference between an artificial medium and a living plant as substrates for fungal growth. Apart from the possibility that any particular plant may be of unsuitable composition for growth of the fungus, there is the main fact that the food contained in a living plant is not immediately accessible to the parasite. It is more or less effectively held up behind the double barrier of a mechanically strong cell wall and a relatively impermeable plasmatic membrane. It is now opportune therefore to consider what mechanism a parasitic fungus possesses for breaking down this double barrier.

First of all there is the power of mechanical penetration to which reference has already been made. This property might conceivably enable a parasitic fungus to force a way through the tissue of a plant and it is not impossible that the mere disturbance due to the physical presence of the hyphae within the cells might lead, in a manner that is not understood, to the death of the latter. In this way the whole resistance of the plant might be broken down by mechanical means only. Then there are chemical agencies. Fungi in the course of their growth produce a variety of chemical substances—acids, enzymes and it may be other types of substances—capable of attacking plant cells. That such substances are in fact produced and excreted by the parasite into the tissues of the host is very obvious in some cases. Microscopic examination shows a more or less pronounced action on the host cells in advance of the hyphae of the parasite, this action taking the form of a disorganisation or rotting of the cell wall sub-

stance and a killing of the protoplast. The resistance of the tissue is broken down by this means and such a parasite is in effect living saprophytically on killed parts of the plant. It is just this feature, viz. the action in advance of the hyphae, that makes possible the physiological analysis of the mode of attack of the facultative parasite. The nature of the active substance concerned may now be considered in some detail.

Apart from special cases, e.g. wilt diseases, in which the active substance has been claimed to be a nitrite, chief attention has been paid to organic acids, more specifically oxalic acid, and the cell wall dissolving enzyme pectinase (or cytase of earlier workers). Almost every conceivable view has been expressed with regard to the relative importance of these two substances. At one extreme, oxalic acid secreted by the parasite has been considered to be responsible both for the dissolving or macerating action on the cell walls and for the killing of the protoplasts. More usually the action on the cell wall has been ascribed to the enzyme and the toxic action to the acid. At the opposite extreme, both actions have been ascribed to the enzyme.

The evidence relative to the oxalic acid theory will be given first. This acid is a frequently occurring product of fungal metabolism. It is formed in greater quantities by some species or strains of fungi than by others, and most strikingly by some strains of *Aspergillus niger*. Even with a suitable fungus, the amount of oxalic acid formed varies very markedly with the conditions of culture. Media rich in glucose and peptone are specially recommended and the temperature should not be allowed to go above a certain point otherwise the oxalic acid is liable to be completely respired to carbon dioxide. Maximum yields are obtained only when the conditions of culture are such that any oxalic acid formed is immediately removed from the scene of the reaction, e.g. by precipitation with a soluble calcium salt. It is important to note this point, since the high figures which have been quoted by some writers for oxalic acid production do not always distinguish clearly between soluble and insoluble oxalate and between soluble oxalate and oxalic acid.

Oxalic acid as such is a fairly active poison to plant cells. Whether this property is due entirely to its strength as an acid (i.e. to H-ion concentration), as has been claimed, or in part to molecules of undissociated oxalic acid, is not clear. The oxalate ion has certainly very little toxic effect, as is shown by the relative harmlessness of neutral soluble oxalates. As regards any action of oxalic acid upon the cell wall substance, this is due to H-ion concentration, and only becomes appreciable when the latter exceeds a certain value.

The best known supporter of the oxalic acid theory is the American worker Smith who claimed that both the dissolving and toxic actions

of *Botrytis cinerea* on lettuce tissue could be explained on this basis. The evidence offered is open to serious objections. There is in the first place no proof that a sufficiently high concentration of oxalic acid is secreted by the fungus, the author relying on a statement of de Bary which had reference to the fungus *Sclerotinia Libertiana* and which furthermore is misinterpreted. De Bary's statement refers to total oxalate, but Smith construes it as oxalic acid.

A further important objection to the oxalic acid theory is to be found in Smith's own results. Even when a solution of the acid, sufficiently concentrated to cause dissolving and killing effects on the tissue, is used, the action does not reproduce that of the fungus. The tissue parasitised by the fungus becomes brown, whereas the acid has a bleaching effect. Smith's interpretation of this difference cannot be accepted. On the contrary the mere fact that oxalic acid interferes with the oxidase colour reaction of the killed tissue proves conclusively that that concentration of acid cannot be present during attack by the fungus.

More recently oxalic acid has been advocated by Higgins as the active principle in the parasitism of *Sclerotinia Rolfsii*. Here again there is, apart from obscurities on critical points, no proof that a toxic concentration of *oxalic acid* is produced by the fungus under conditions comparable to those which obtain in the neighbourhood of the invading hyphae.

The objections to the oxalic acid theory just given do not exhaust the list. It has been pointed out, for example, that if secretion of acid is the factor responsible for parasitism, such a fungus as *Aspergillus niger*, which is particularly notable in this respect, should be an active parasite—which in fact it is not. I do not consider that this objection is necessarily insuperable, or at any rate, as I shall show later, the protagonist of the enzymic theory has very much the same difficulty to explain away.

With some fungi at least there is definite proof that the active principle is not oxalic or any other acid. Thus the parasitic action of *Botrytis cinerea* can be imitated exactly by an extract of neutral reaction, which furthermore contains no trace of an oxalate. Again many parasites (e.g. species of *Fusarium*, *Pythium de Baryanum*, certain plant pathogenic bacteria, etc.) have a strong tendency to develop an alkaline reaction in growth and in fact induce an alkaline or at most a faintly acid reaction in parasitised tissue.

Where a distinctly acid reaction is produced during fungal invasion or where the parasitism of a fungus is favoured by the addition of an acid, it does not follow that the acid is the agent primarily responsible for attack of the tissue. One may equally reasonably suggest that acidity favours the action of the active principle, which is another substance altogether.

My own view with regard to the importance of oxalic acid in connection with parasitism is that in no case has satisfactory evidence been brought forward, while in many others there is convincing evidence against it. It is insufficient to point out that such and such a fungus produces large quantities of this acid when grown in culture for several weeks on media of specially arranged composition, for example on media of high sugar content. It must be remembered that spores of a parasitic fungus when placed in water on the surface of a plant normally begin to attack within a day or so, and it is under these restricted conditions that the secretion of an effective concentration of oxalic acid must be demonstrated. As the toxicity of oxalic acid appears to be due mainly to its acidity, the technique involved is simple. No clear proof along the lines indicated has yet been given.

There remains the alternative theory that the enzyme pectinase is the active principle of parasitism. So far as concerns its occurrence, there is good *a priori* evidence. Its formation has been demonstrated for many fungi, in my own laboratory for some dozen species which have been studied in this connection. The difficulty here is rather of another kind, viz. that this enzyme is also secreted by mere saprophytes, and that there is no correlation between the amount of enzyme which can be demonstrated under standard conditions and the parasitic vigour of the fungus. This point will be taken up more fully later.

It appears to me to be obvious that where definite rotting of the parasitised tissue occurs—and this effect is shown with greater or less distinctness with the vast majority of parasites of the facultative type—the enzyme pectinase must be present. The majority of workers from de Bary onwards have accepted this view. The enzyme has been considered to be responsible for the attack upon the host cell walls, while the nature of the toxic principle has been left open. The most detailed examination of this point was that carried out by myself some years ago, where it was shown for the fungus *Botrytis cinerea* that the macerating and toxic principles, if they are different, are both colloidal thermolabile substances which are strikingly similar in their response to  $\text{pH}$  concentration, to deactivation by heat or mechanical agitation and in their diffusive capacities through certain membranes. As was pointed out at the time, the evidence available can be interpreted in more than one way, but the simplest hypothesis is that the two manifestations of activity are due to the same substance. Certain implications as to protoplasmic structure would arise from this conclusion, but these do not concern us here. The further consideration of the enzymic theory will be taken up later.

A survey of the interplay between host and parasite when brought into intimate contact with each other may conveniently be given

from the point of view of the kind of resistance which the host may offer. I propose to distinguish five types, largely because concrete examples of each can be given. With advancing knowledge, a finer classification will no doubt be possible. The types of resistance are as before, mechanical and chemical, and the latter is further subdivisible into four categories.

### (1) Mechanical resistance

A familiar example of this is seen in the limiting of fungal invasion by the lines of vascular bundles with their accompanying fibres (e.g. in grass leaves). More familiar still to plant pathologists are the various structures such as cork layers, gum barriers, callosities etc. which are formed by the host in response to wounding. That these do in fact place an utmost limit to the fungal invasion cannot be doubted, though it might fairly be suggested that in some cases at least invasion had already been stopped by some chemical factor. Whether the wound response is conditioned solely by the host or whether excretions from the fungus play some part is not known. It is not impossible for instance that some parasites may have the power of suppressing cork formation, being able by that means to parasitise the tissue throughout. The physiology of cork formation is obviously one of live interest to the plant pathologist.

A general correlation is sometimes indicated between the percentage of cell wall substance of plants and resistance to fungal disease. For example, it appears to be a fairly good rule that cultivated forms of plants are more susceptible to a variety of fungoid diseases than are their wild prototypes. As cultivation has often led to the development of soft fleshy or succulent structures, it has been plausibly held that resistance is correlated with a greater average thickness of the cell walls and conversely. More specifically it has been claimed that this factor of mechanical resistance explains the different degrees of varietal resistance of plums to *Sclerotinia* (Valleau) and of potato tubers to *Pythium deBaryanum* (Hawkins and Harvey). As both the diseases mentioned are characterised by very distinct rotting of the tissues, it is incontestable that enzymatic action is concerned. I should doubt therefore whether mechanical resistance is really operative, and would suggest that the true factor of resistance is a chemical one which is correlated with the development of thicker or more rigid walls. As fungi do possess the power of mechanical penetration, one cannot say offhand just how far the physical factor supports the chemical one, and it is probable that their relative importance varies from one disease to another. Inasmuch as plant pathogenic bacteria cannot be considered to possess any means of mechanical penetration, it is obvious that the chemical mechanism is all-important in their case, and, as the course of a bacterial disease

is essentially similar to that of a fungal one, it is perhaps safe to discount the mechanical factor, at least in any case where enzymatic action is clearly marked.

### (2) Chemical resistance

Four types can be distinguished here, and these will be dealt with in succession.

(a) The composition of the plant may be such as to be unsuitable for the growth of a particular fungus. This type of resistance will be illustrated by a number of examples.

High acidity of the plant sap has been given as the factor which protects certain plants or plant parts against some fungi, and there is no doubt that this is sometimes a satisfying explanation. Thus it is clear that only fungi with a high acid tolerance could parasitise such acid structures as unripe apples or plums, and on examination one finds that *Monilia* spp., which parasitise these fruits, have a remarkably high acid tolerance. The factor of acidity has also been used in explaining the mode of invasion of certain citrus fruit parasites (e.g. *Pythiacystis*) which more or less avoid the acid succulent hairs but ramify through the central axis, dissepiments and pericarp.

It is difficult to believe, however, that acidity of the plant sap, as a factor repressive to fungal growth, can have any wide application. The acid concentration of the vast majority of plant tissues is well within the limits for good growth of most fungi. While high acidity of a particular plant would restrict parasitism to such fungi as preferred a highly acid reaction or at least tolerated it, with perhaps a tendency to reduce the amount of acid and thereby to create more favourable growth conditions, this factor is quite inadequate to explain the resistance of a plant with more usual composition. More particularly, it offers no basis on which to construct a theory which would explain the degree of selectivity shown by the facultative type of parasite. In passing it may be noted that all attempts to explain the specialisation of obligate parasites such as rusts on the basis of fine differences in *pH* concentrations of the host plants have similarly ended in failure.

The presence in the plant of particular substances which act as poisons or inhibitors to fungi has also been cited as explaining resistance to attack. Such substances are oils, esters, tannins, etc., either present as such or produced in the lesion in response to wounding. It is well known, for example, that the volatile principle of onion bulbs is highly repressive to the growth of fungi in general, while those fungi which do parasitise onion show relative tolerance. In this connection may also be quoted the observed association of resistance in some plants with the presence of a particular colour. That the agent responsible for resistance is not the pigment itself but a

substance associated with it has been shown recently by workers in the Madison laboratory. The resistance of certain coloured varieties of onion to the "smudge" fungus (*Colletotrichum circinans*) has been proved to be due to the presence of an organic substance of ascertained constitution.

Now while the search for inhibitory substances and the like has yielded some measure of success, I do not believe that any general solution of selective parasitism is to be found along these lines. The relationship to be explained is a reciprocal one, of the type indicated in the scheme already put before you (p. 18), with the symbols + and - now meaning respectively ability and inability to parasitise. If fungus *a* attacks host *A* because there is no repressive substance present in *A* whereas host *B* is not attacked because it contains such a substance, how is one to explain the behaviour of fungus *b*? One could, it is true, get over the difficulty by postulating two repressive substances to which the two fungi were unequally sensitive. While there is some degree of selective action by poisons upon fungi, the main truth is that toxicity is a fairly absolute property, so that it is more than doubtful if any satisfactory explanation is to be found on the basis of special toxic or repressive substances. I therefore look upon the type of resistance under consideration as being limited to special cases only.

(b) A second type of chemical resistance is seen where the composition of a plant is such as to allow ready growth of a fungus but not the secretion in appreciable quantity of the active substance. At the moment I can quote only one definite instance of this kind of resistance, viz. that of the apple fruit to various fungi. The controlling factor appears to be low nitrogen content of this fruit.

Vasudeva found that the fungus *Botrytis Allii*, which normally is not parasitic upon apples, produces definite attack if supplied with a small quantity of a variety of nitrogenous substances. From the point of view of spore germination or of mycelial development, apple extract, at any concentration from full strength downwards, is perfectly suitable for the fungus in question. The significant difference is that whereas no detectable pectinase enzyme is formed when apple extract is used as nutrient, it is very definitely present when a trace of nitrogenous substance is added to that medium. It appears therefore that resistance of the fruit is based upon its very low nitrogen content, not as repressing growth but enzyme secretion. It may be added that a slight increase of nitrogen supply likewise enhances the parasitic vigour even of a pronounced apple parasite like *Monilia fructigena*. Presumably therefore the difference between these two fungi, as regards attack of apple fruit, is that the latter produces an effective secretion of pectinase at a lower concentration of nitrogen in the substrate than does *Botrytis Allii*.

Horne has likewise shown that there is a high inverse correlation between the nitrogen content of different individual apples of the same variety and the rate of invasion by a parasitic fungus.

(c) The third type is to my mind by far the most important of all. The composition of the plant is such as to favour fungal growth, and also, as far as can be seen, to allow of secretion of the pectinase enzyme; nevertheless there is no attack. This may be described as the case of the average fungus, *i.e.* with no special food requirements or special sensitiveness or tolerance to chemical substances, and the average plant, *i.e.* with no special inhibitory constituent.

A particular example of this type of resistance is that of potato tuber tissue to *Botrytis cinerea*\*. This fungus grows vigorously on potato decoctions of widely varying strength, and on pieces of potato tuber which have been autoclaved, or steamed or chloroformed or frozen. From any one of these media a preparation can be made which actively destroys pieces of potato tissue when immersed in it. When spores of *B. cinerea* are placed in a wound on potato tissue they germinate vigorously. On the enzyme theory, every necessary condition appears to be fulfilled. Nevertheless attack is slight or negligible.

The difficulty seems to be even greater when one compares *B. cinerea*, a non-parasite of potato tuber, side by side with *Pythium deBaryanum*, an active parasite. Preparations of pectinase enzyme can be prepared from the latter fungus, but so far under much more restricted conditions than from *Botrytis cinerea*. Thus while good enzymic extracts may be obtained from cultures of *Pythium* on living or dead potato tubers, cultures on potato decoction give inactive or very feebly active preparations. On the latter medium *Botrytis cinerea* gives very active preparations, either in the medium itself or by extracting the young mycelium.

The readiness with which a fungus secretes the pectinase enzyme does not therefore give any reliable index of its parasitising ability. The same difficulty has already been pointed out by a number of workers. Thus Harter and Weimer could find no correlation between the parasitic vigour of different species of *Rhizopus* and their capacity to furnish active enzymic solutions under standard conditions. The same conclusion was reached by Paul for a number of strains of *Botrytis cinerea*.

A satisfactory explanation of the basis of resistance in the case under consideration thus gives a critical test of the enzymic theory of

\* As the host-parasite relationship is probably somewhat delicately balanced, it is not unlikely that some strains of *Botrytis cinerea* may be able to attack potato tissue under a wider range of conditions than do the strains which have been used in my laboratory.

In the remainder of this paper I shall have occasion to refer frequently to a number of unpublished researches which are in progress, chiefly by M. P. Hall, K.P.V. Menon and M. Fernando.

parasitism. While it is not yet possible to give a complete story, even for a single fungus and host, several points have emerged in recent work which make the difficulty less formidable.

Up till fairly recently certain assumptions have been made with regard to fungal pectinase, and these now require considerable overhauling. From my own work it was known that pectinase is secreted (and excreted) from the earliest phases of spore germination onwards; that under a given set of conditions the quantity present in a culture increased up to a maximum and then slowly diminished. In the lack of any better information, one assumed that there was a certain proportionality between vigour of growth and rate of excretion of the enzyme. Another assumption was that pectinase had the same properties under all conditions and that the pectinase of one fungus was the same as that of any other, though as a matter of fact I knew long ago that the pectinase of *Botrytis cinerea* had very different properties from the pectinase (=cytase of Brown and Morris) of the germinating cereal grain. Further work has shown that everywhere there are greater complications.

The activity of the enzymic solution obtained from a fungus under standard conditions would be a measure of parasitic vigour only in so far as there was some proportionality between the rates of enzymic excretion under different nutrient conditions. To refer to the two fungi quoted above, if *Botrytis cinerea* produces a stronger enzymic solution when grown on potato extract than does *Pythium deBaryanum*, is one justified in assuming that the same applies when the fungi are placed on the cut surface of living potato tissue? There is an increasing body of evidence to the effect that the quality and quantity of nutrients has an important influence on the amount of enzyme excreted. It has recently been shown that, over a certain range of concentrations, there is a negative correlation between amount of growth and enzymic excretion, the controlling factor being largely the carbon/nitrogen ratio of the medium. When the ratio is very high there is luxuriant growth but very feeble excretion of enzyme; when the ratio is very low, the amount of growth may be negligible but abundant enzyme is formed. A somewhat similar point has already been referred to in *Botrytis Allii* in relation to apple fruit. These findings—that the nitrogenous constituent has a markedly intensifying influence on secretion of pectinase—fall into line with general experience that nitrogenous manuring typically increases susceptibility to disease.

The quality of carbonaceous food appears also to be of importance. Thus *Pythium deBaryanum* produces negligible or considerable amounts of enzyme when grown on potato decoction or tissue respectively. There is here a suggestion that the occurrence of pectic substances in the substrate intensifies the production of pectinase. Harter and

Weimer likewise found that the presence of pectin in the medium intensified the secretion of pectinase by species of *Rhizopus*. The work of Dickson and collaborators on the resistance of wheat seedlings to *Gibberella Saubinetii* appears to be capable of a similar interpretation. It was found that under one set of conditions the seedlings developed cell walls of a more definitely pectic nature than under other conditions. The former were susceptible to blight and the latter were not.

A first point then is that there is some specificity in the secretion of pectinase, and the precise conditions have obviously got to be worked out for each particular fungus before any valid quantitative comparisons can be made.

A second point is that the detailed properties are not the same for pectinase as prepared for different fungi or even as prepared under different conditions from the same fungus. Chona showed that whereas the enzyme of *Botrytis cinerea*, extracted from germinated spores, was favoured in its activity by an acid reaction but was highly sensitive to the presence of certain salts, the enzyme of *Pythium deBaryanum* had its optimal activity in an alkaline medium and was relatively tolerant to the salts in question. Later Menon demonstrated definite differences between pectinase enzyme as prepared from *Monilia fructigena* grown on different media.

The latter evidence tends to discount the view that there are possibly an indefinite number of types of pectinase. A more plausible hypothesis is that it is the same pectinase in all cases, but that the enzyme has some of its properties modified by association with substances in the medium. As the differences quoted above persist after the enzyme has been purified to some extent by precipitation with alcohol, adsorption phenomena are suggested. Work in progress is giving results in conformity with the provisional rule that the pectinase enzyme is less sensitive to a particular substance when secreted in the presence of that substance. In accordance with this rule the enzyme is favoured by an acid or an alkaline reaction according as the conditions of culture are such as to tend to acidity or alkalinity as growth of the fungus proceeds. Much further work will be required before it is seen how far this rule applies and what are its limitations. Its importance lies in this, that to some extent at least a fungus is able to adapt its enzymic mechanism to deal with a plant containing substances which might appear to be antagonistic to the action of the enzyme, if the latter were used in some standard form.

A third point, which may not be independent of the last, is that, even when active enzyme is known to be present, there may be negligible attack of a susceptible tissue under certain conditions. An illustration will make this clear. A sample of *Botrytis* enzyme is tested by immersing standard discs of potato tissue in it and found to be very active. When drops of the same preparation are placed

on the freshly cut surface of a potato tuber, they are found to be quickly absorbed by the tissue (which has a certain avidity for water, even when normally turgid) and very little rotting is produced. If however the tissue is previously injected with water so that it is completely turgid, drops of the enzyme solution produce very considerable rotting. In this connection it is very illuminating to note that the fungus itself behaves similarly, viz. that when its spores are placed on subturgid tissue there is no attack, whereas when the tissue is fully turgid attack is very definite. The similarity in the behaviour of fungus and enzyme gives strong ground for the belief that the enzyme is in fact the essential part of the parasitising mechanism.

The failure of *Botrytis cinerea* to attack ordinary potato tissue is now somewhat understandable. Even if any enzyme is formed under these conditions—which is not certain—it would fail to act, in accordance with what has been said above. What happens to the enzyme when the tissue absorbs water from the drops laid on, and why it fails to produce any rotting are points that require further study. A point of more immediate importance, however, is to explain why *Pythium deBaryanum* or *Phytophthora erythroseptica* under the same conditions produces an enzyme which *does* attack the tissue. As a working hypothesis I would suggest that the difference is to be sought in the other metabolic products of the fungi. It has been shown that a factor making for resistance is the capacity of the living tissue to absorb water from the neighbourhood of the fungus, thus paralysing in some way the enzyme. Presumably there is some substance or substances formed by *Pythium* which counteract this absorptive effect. Further work will show how far an explanation can be found along this line.

The water exchange between fungus and host is probably a factor of first class importance in conditioning parasitism. It is of course common knowledge that moist conditions are necessary for the initiation of attack, but one usually assumes that the moisture functions merely by allowing germination and penetration. Once the fungus has become established inside, moisture conditions are supposed to be less important. There are numerous observations, however, which fall into line with the hypothesis that a turgor deficit within the tissue confers resistance. This has been shown, for example, in quantitative studies of the rate of attack of apples by *Monilia fructigena*. Conversely it has been found by various workers that many fungi attack a wider range of plants under laboratory conditions than in nature. The unnaturally humid conditions which are set up in laboratory experiments may well afford the explanation. Again many seed-borne fungi show a behaviour which could best be explained in terms of moisture relationships. If conditions are such that the plant is turgid, attack progresses; if there is subturgor, the fungus, though it may

have entered, is unable to progress to the extent of making a macroscopically visible lesion, but remains dormant until such time as sufficient turgor is again established. The limited spread of the shot-hole type of lesion and even of a disease like apple scab would be explained on the same basis. I would also suggest that the difference between a soft rot and a hard rot rests upon a different water balance between parasite and host in the two cases. The soft-rotting organism retains in its surroundings sufficient water to enable enzymic decomposition to proceed to completion whereas in a hard rot enzyme action is arrested at some intermediate stage. Viewed in this light, a hard-rot indicates a less developed parasitic mechanism than does a soft rot, and accordingly I would consider the following list of parasites as forming a series of increasing parasitic capacity in relation to potato tissue: *Botrytis cinerea*, *Phytophthora infestans*, *P. erythroseptica*, *Pythium deBaryanum*.

(d) A fourth type of chemical resistance is that in which the active principle of the fungus is unable to affect the tissue of the plant. Certain mosses and hepatics have been found to possess this type of resistance to the fungus *Botrytis cinerea*. These may be overgrown by the mycelium of the fungus or may be heavily sprayed with spores under conditions favourable for attack, without a trace of injury appearing. Similarly an enzyme solution of the fungus produces no effect on these tissues. One may look upon this case as illustrating a more fundamental and absolute type of immunity than anything discussed above. The cell wall substance of the plant is not hydrolysable by the enzymic apparatus of the fungus. As the best evidence available indicates that the protoplast-destroying agent only functions after previous attack on the cell wall by the enzyme—if in fact the two substances are not the same—there is likewise no attack on the living cells. Immunity thus ultimately rests upon the composition of the cell wall. The chemistry of cellulose, hemicellulose, pectin and such like substances is therefore of the very greatest interest to the student of disease resistance.

Reviewing the enzymic theory of parasitism, as applicable at the moment to the facultative type of parasite, one must confess that it is somewhat complex. The excretion of enzyme varies, quantitatively and qualitatively, according to the nutrient conditions prevailing, and even if these are such as to allow of the process, the enzyme may be prevented from working by forces exerted by the living host cells. There is room here for a considerable interplay of factors, and it is just this complexity of action which makes the enzyme theory a promising one. Any theory that aims at some measure of generality must explain why a particular plant, though containing food substances perfectly adequate for the growth of a multitude of cultivable

fungi, is nevertheless parasitised by only very few. It must also explain the more delicate problem of environmental effect on parasitism, viz. that under one set of conditions attack progresses, and under another is stopped. From the point of view of the fungus it must explain why one fungus is able to attack and another not. It must, at one and the same time, be capable of explaining enough but not too much. With these requirements it is plain that a theory resting simply upon the presence or absence of a toxin, either in the parasite or the host, would not lead very far. It is much more likely that fungi as a class have essentially the same mechanism of attack, but that the parasitic vigour shown on any particular plant is determined by quantitative considerations.

In discussing the enzymic theory I have indicated certain features of the mode of action because there is some experimental evidence for the same. The evidence is as yet very fragmentary and it is more than probable that, apart from criticisms which anyone else may offer, I shall see fit to modify some of the views expressed in the light of further work. I set out, however, not merely to review the present state of knowledge on the subject of disease resistance, but to indicate in what directions research could be directed. The latter purpose could not be achieved without some lapses into speculation. This address will have served its purpose if it has shown that there is still a very wide and practicable field of academic study to be explored in the physiology of parasitism.

## ISARIA

By T. PETCH

THE name *Isaria* was first used by Hill in his *History of Plants* (1751), p. 66. The relevant passages of his account are quoted below, references to male and female flowers being omitted.

"*Isaria* is a genus of Fungi, consisting of stalks of a simple or rameous figure, formed of a circular series of fibres, arranged round a cavernous axis, and each fibre having at its end a capsule.... The *Isariae* are all very small plants, and the surface of them all is alike of a beautiful granulated structure, it being all composed of globular bodies, applied as closely as possible to one another.

"Micheli met with two species of this genus, which he very justly distinguished from all other fungi, under the name *Puccinia*.... We have called the genus, *Isaria*. From the Greek, *is*, a fibre, these being the only known fungi that are composed wholly of fibres, supporting the fructifications."

Hill's conception of *Isaria*, as is evident from Micheli's figures, is a fungus with a hollow clava, which bears spores at the ends of threads which are perpendicular to the clava. In transverse section of the clava, Micheli showed the "threads" of *Puccinia* as radial. Hill took over Micheli's genus and changed the name; and as far as Hill knew, *Isaria* Hill is a synonym of *Puccinia* Micheli.

Hill's first species was his own "*Isaria ramosa varie divisa*. The variously, divided, rameous *Isaria*," which he described as follows:

"This is an extremely beautiful little plant. It rises with a single stem rounded, and of the thickness of a small packthread; this runs up single to about a third of its height, and from thence begins to divide into a number of lesser branches: these ramify again, and at length the whole forms a kind of little bush with the branches, all erect, and terminating in obtuse points. The whole plant is of a deep orange colour, and its height is more than half an inch. The surface of the branches, when examined with a microscope, appear beautifully and regularly granulated: when cut transversely, and examined, they are found to consist of a cylindric, cavernous core, around which are ranged series of fibres very short and slender, each, at its extremity, supporting an oval body....

"This beautiful fungus is common in Charlton Forest in Sussex, growing to the decaying bodies of beeches and other trees. I never saw it elsewhere, nor has any author described it."

Hill also included in his genus two species which he took from Micheli, *Nova Plantarum Genera*, viz. *Isaria simplex*, which was Micheli's *Puccinia non ramosa major pyramidata* (Micheli, tab. 92, fig. 1), and

*Isaria ramosa bifida*, which was Micheli's *Puccinia ramosa*, *bifurcata omnium minima* (Micheli, tab. 92, fig. 2).

Micheli's species are known. The first is a *Gymnosporangium*, and the second a Myxomycete, *Ceratiomyxa fruticulosa*. But the type species of Hill's genus, according to modern views, is his *Isaria ramosa varie divisa*, and no one appears to have made any attempt to identify it. The only solution which suggests itself after reading his description is that it was *Calocera viscosa*. In any case, Hill's conception of *Isaria* is widely removed from that of the present day.

Linnaeus, *Systema Naturae*, Ed. 13 (1791) by Gmelin, did not include *Isaria*.

Persoon, *Dispositio Methodica Fungorum* (1794), included *Isaria*, with the generic description, "Erecta subramosa, pilis densis laevibus pulverulentis obsita," and two species, *Isaria mucida* and *Isaria agaricina*. The first of these is again *Ceratiomyxa fruticulosa*, while the second is *Isaria brachiata* (Batsch) Schum. Persoon did not refer to Hill, but there is no doubt that he took the name *Isaria* from him. He returned Hill's second species to Micheli's genus *Puccinia*, and retained the third species in *Isaria*. Evidently he could make nothing of the "type species."

The *Dispositio* was republished in 1797, as *Tentamen dispositionis*, etc., with a supplement in which Persoon extended his definition of *Isaria* to "Erecta simplex furcatimque divisa, pulvere farinaceo aut pilis densis obsita."

Meanwhile, Persoon had written his *Commentatio de Fungis Clavaeformibus*, which was also published in 1797. In this he gave the generic description of *Isaria* as "Byssoidaea simplex ramosaque, pulvere farinaceo utplurimum obtecta." The first species mentioned was *Isaria crassa* Pers., which is usually taken to be one of the forms of *Isaria farinosa*. He still, however, retained *Isaria mucida* in the genus.

In Persoon, *Synopsis Methodica Fungorum* (1801), the generic description of *Isaria* is "Subbyssoidaea, simplex ramosaque, pulvere farinaceo (subfilato) obtecta. (Substantia molliuscula. Color albus)." The type species is again *Isaria crassa*, *Isaria mucida* being the third in the list and *Isaria agaricina* the fourth.

In 1805, Albertini and Schweinitz (*Conspectus Fungorum*) instituted a new genus, *Ceratium*, for *Isaria mucida* Pers., and enumerated *Isaria*, without any generic description, with *Isaria crassa* as the first species. As they cited only Persoon, *Synopsis*, in this connection, they would probably have been unaware that they were transferring the original type species of Persoon's genus, even if the idea of type species had ever occurred to them.

Link, *Observationes* (1809), described *Isaria* as "Stroma elongatum, simplex, clavatum, aut ramosum, carnosum lignosumque, floccis tectum simplicibus ramosissime. Sporidia floccis inspersa," and added the species, *Isaria velutipes* Link, which is now taken to be one of the forms of *Isaria farinosa*.

Nees, in *System der Pilze* (1817), gave a long account of the genus *Isaria*, and placed as his first species, *Isaria bulbosa* Nees. His account of the genus shows that he had the modern idea of it, but his species has never been identified again. Link (*Species Plantarum*) suggested in 1825 that it was a juvenile condition of *Isaria glauca*; and Lindau (*Rabenh. Krypt.-Fl.*) stated that the description was so indefinite that it had better be discarded.

Persoon, in *Mycologia Europaea* (1822), accepted the genus *Ceratium* A. & S. He again altered the generic description of *Isaria* to " *Elongata, subclavaeformis, simplex ramosaque, sicca, floccoso-furfuracea. (Color plerumque albus.)*" His first species was now *Isaria truncata*, which had been placed second to *Isaria crassa* in *Synopsis Methodica Fungorum*, but as these are regarded as synonymous the change is immaterial.

In *Species Plantarum*, Ed. 4 (1825), Link altered his generic description to " *Thallus dense contextus. Sporodochium elongatum simplex aut ramosum, superne floccosum. Sporidia floccis inspersa,*" and added the note " *Sporidia globosa semper minuta.*" He placed first, *Isaria crassa* Pers., with *I. truncata* Pers. and *I. velutipes* Link as synonyms.

Fries, in *Systema Orbis Vegetabilis* (1825), included " *Isaria* Pers. *Receptaculum elongatum, continuum, simplex aut ramosum, siccum, persistens, floccis obductum. Sporidia globosa, floccis inspersa. Coloratae, saepius albae,*" but cited Nees, *Syst.*, p. 85. In *Systema Mycologicum III* (1832), he wrote " *Isaria* Hill ex em. *Receptaculum elongatum, contiguum, e floccis dense intricatis coalitum. Flocci sporidiiferae investientes, patentes. Sporidia globosa, simplicia, inspersa.*"

Persoon (except in the *Dispositio*) and Link had emphasised the entomogenous nature of some of the *Isariae* by placing the entomogenous species first in the genus. Fries, however, discarded that arrangement and placed first the species which grew on the ground and on dung, beginning with *Isaria terrestris* Fries, which he stated was not indeed one of the largest species, but was pre-eminently typical and distinct.

Saccardo, in *Michelia II*, 32 (1880) cited *Isaria* Hill, with the type species, *Isaria farinosa* Fr. In *Sylloge Fungorum IV* (1884), he cited *Isaria* Pers., *Tentamen*, with the same type species.

Lindau (*Rabenh. Krypt.-Fl. IX*) also cited *Isaria* Pers., *Tentamen*, but placed as his first species *Isaria intricata* Fr.

*Isaria* Hill is, by intention and as far as can be definitely determined, a synonym of *Puccinia* Michelii. Hence, if the rule "Once a synonym always a synonym" is adhered to, the name *Isaria* cannot be used again.

*Isaria* Persoon, *Dispositio* (1794) and *Tentamen* (1797) is, by the method of type species, a Myxomycete.

*Isaria* Persoon, *Commentatio* (1797), *Synopsis* (1801), *Mycologia Europaea* (1822), and *Isaria* Link, *Species Plantarum* (1825), is a fasciculate or concrecent *Spicaria*.

*Isaria* Nees, *System der Pilze* (1817), is indeterminable.

*Isaria* Saccardo, *Michelia* (1880) and *Sylloge Fungorum* (1884), is a fasciculate or concrecent *Spicaria*, as far as regards the type species, but it is not *Isaria* Hill (1751) nor *Isaria* Persoon, *Tentamen* (1797).

*Isaria* Lindau (1908) is again not *Isaria* Persoon, *Tentamen* (1797), nor is it equivalent to any other author's *Isaria*, since *Isaria intricata* Fries is not a fasciculate *Spicaria*. It might, however, be argued that *Isaria* Lindau is equivalent to *Isaria* Persoon, *Tentamen*, *emend. A. & S.*, since the removal of *Isaria mucida* left only *Isaria agaricina*, which is co-generic with *Isaria intricata* Fr. But Albertini and Schweinitz dismembered *Isaria* Persoon, *Synopsis*, not *Isaria* Persoon, *Tentamen*.

*Isaria* Fries, *Systema Mycologicum* (1832), has for its type species *Isaria terrestris* Fr., which was described as "*Simplex, aequalis, basi villosa nigrescens, apice dilatata truncata alba, floccis sporidiiferis vestita*," with a further long explanatory note. It was collected in Sweden, on bare ground on hill sides in beech woods, and does not appear to have been recorded since. By the courtesy of the officers in charge of Fries's herbarium, I have been furnished with a slide made from the type specimen.

The synnemata either arise from a brown conical base, or several strands, up to 0.15 mm. broad and composed of parallel brown hyphae, arise separately from the substratum and converge, uniting at a height of about 1 mm. to form the synnema. The latter is about 3 mm. high, with a brown central column of parallel hyphae, up to 0.4 mm. diameter, surrounded by a weft, up to 0.25 mm. thick, of loosely interwoven, contorted, thick-walled, brownish hyaline hyphae. Towards the apex the colour becomes brownish white, the synnema expands, and the apex is abruptly truncate, the synnema growing out in a flat expansion perpendicular to the axis of the column, on one side only (in my specimens). On the upper surface of this expansion the hyphae are regular, in continuation of the regular hyphae of the central column; on the lower surface, they are irregularly contorted and interwoven, like those of the exterior of the column. There are no conidiophores or conidia. On a few free brown hyphae which run into the bases of the synnemata, clamp connections are present, but it is doubtful whether these hyphae are those of the *Isaria*.

There would appear to be two possible explanations of the truncate apex—one, that the synnemata encountered some obstacle which changed their direction of growth; the other, that the fungus is a developing Hymenomycete, and that, as in *Septobasidium*, the lateral growths from the apices of the synnemata would fuse with one another and produce a hymenium. There is nothing in the specimen to show that it is a Hymenomycete. It would appear to be more probably the initial stage of a Hymenomycete. But the question can be decided only by finding it again in the type locality and watching its development.

Thus, Fries's type specimen is indeterminable, and consequently we cannot cite *Isaria* Fries (1832). To retain the name *Isaria* for a genus of Mucedinaceae, we must cite *Isaria* Persoon, *Commentatio* (1797) or *Synopsis* (1801), with the type species, *Isaria farinosa* (Dicks.) Fr., of which *Isaria crassa* Pers. and *Isaria truncata* Pers. are synonyms.

There is another, and more important, aspect of the question, what is *Isaria*. The prevailing idea of the genus since the time of Persoon has been an erect fascicle of mucidinous, amerosporous conidiophores united, in part, into a stalk or clava of varying height. Many species included in *Isaria* do not agree with that conception, but have been placed in the genus merely because they grew on insects. That was perceived by Persoon, who adopted the genus *Ceratonema* for *Isaria sphecophila* Ditm. But, excluding such obvious misfits, the genus has been a centre for species which agree only in their most general shape. It is a form genus in the widest sense of the term, more general than *Agaricus* when used for all lamelliferous Hymenomycetaceae, and almost as unscientific as *Clavaria* in the sense of Holmskiold.

The unsatisfactory nature of the genus was evident to Fries, who remarked that it embraced species which differed from one another in structure and in the mode of origin of their spores. It would appear that the type of conidiophore is of greater importance in classification than the fact that the conidiophores are united. In identifying an *Isaria*, the type of conidiophore should be the primary diagnostic character, and it is almost impossible to interpret the descriptions of very many species of *Isaria*, because the type of conidiophore has not been recorded.

Presuming that the genus *Isaria* is retained, with *Isaria farinosa* as the type species, then *Isaria* is a compound *Spicaria*. Species which have a different type of conidiophore cannot remain in the genus, and a large number of other genera will have to be instituted for them. That, indeed, will happen, whatever species is taken as the type. But the isarioid form is not necessarily an invariable feature of a species. *Isaria farinosa*, for example, frequently occurs as a simple *Spicaria*, and conversely, *Beauveria densa* may take the isarioid form. Nor have all isarioid species been consistently placed in *Isaria*; *Botrytis Tilletii*, for example, is an *Isaria* in the wide sense in which the name has hitherto been used.

It would seem simpler to discard the genus *Isaria*, and to distribute the species among the corresponding mucidinous genera. In most species, the type of conidiophore agrees with one of the established genera of Mucedinaceae. The name *Isaria* might be retained as a descriptive term, parallel to *sporodochium* and *synnema*, or it might be used to distinguish the isarioid species of a genus, e.g. *Spicaria (Isaria) farinosa*.

## AN EVOLUTIONARY STUDY IN AGARICS: *COLLYBIA APALOSARCA* AND THE VEILS

By E. J. H. CORNER, M.A.

*Botanic Gardens, Singapore*

(With 13 Text-figures)

A PROBLEM which must be solved before the evolution of agarics can be understood is the nature of the veils. They are considered advanced features and genera are based on the degree of their development. Primitive genera, as *Clitocybe* and *Paxillus*, have no veils; others, such as *Tricholoma* and *Hebeloma*, have a thin universal veil, which is thicker and developed to a marginal veil in *Armillaria* or *Pholiota*; in the most advanced, as *Amanita*, there are universal, marginal and partial veils. But in many genera, such as *Naucoria* and *Boletus*, these distinctions are merely sectional and, more perplexing still, in several groups of common and by no means primitive agarics they are specific or even subspecific. For instance, both *Armillaria mucida* (Schrad.) Fr. and *A. mellea* (Vahl) Fr. have a thick universal veil leaving a ring on the stem, and *Collybia radicata* (Reh.) Berk. and *Clitocybe tabescens* Scop. are gymnocarpic without a veil: yet *Collybia radicata* is closely allied to *Armillaria mucida*, and *Clitocybe tabescens* differs in no other respect from *Armillaria mellea*. Further, *Amanita gemmata* Fr. (12) has two forms equally abundant, one, *Amanitopsis adnata* (W.G.Sm.), Sacc. with a universal veil and volva, and the other, *Amanita junquillea* Quél., with a partial veil and ring in addition. Clearly the evolution of the veils has been polyphyletic and homoplastic, and each species needs separate investigation.

I have been enabled to approach the problem in the *Collybia radicata*—*Armillaria mucida* group by an investigation of *Collybia apalosarca* B. & Br., which is intermediate in many respects, structural and biological, between the two and it has a rudimentary veil. I have examined the structure of the mature fruit body of the Malayan form of *C. radicata*, though I have been unable to work out the development—even to find young ones—on account of its sporadic and solitary mode of growth in this country. Fischer's morphological description of *Armillaria mucida* is brief, and as the species is a temperate one it was not available for study in Malaya.

*Collybia apalosarca* is common in the eastern tropics, and has received many names. It was placed in *Pluteus* and *Phaeolimacium* by Hennings and in *Oudemansiella* by v. Hoehnel, in which respect he is followed by Petch (19), but it is preferable in our present knowledge of generic

limits in Basidiomycetes to conform with the straightforward Friesian classification and to retain the original combination. As Petch has dealt in full with the history and synonymy of the species, it need not be recounted save to remark that *Mucidula alpithophylla* (B. & Curt.) Pat., from the description, is certainly the same. I identified the Malayan material from Petch's description; that which is given here is based on the Malayan material which differs in no essential.

In Malaya *Collybia apalosarca* occurs on dead wood in the lowland forest, though it may be found in estates and gardens in very wet weather. It is particularly abundant in the rainy season in forest reserves where the second class trees have been ringed and left to die; tufts of fruit bodies then develop on the dead standing trunks at all heights up to 50 ft. from the ground, and from a distance they have very much the appearance of the "beech-tuft." It does not grow from underground wood and is never terrestrial as *C. radicata*. It is probably abundant in the mountains also, since I found it frequently at 4000 ft. on Fraser's Hill, Pahang, and at a similar elevation at Brastagi in Sumatra: it is odd, therefore, that it has not been reported from south temperate countries.

The material for the developmental study came from a felled trunk of *Araucaria* on Government Hill in Singapore. A large section, 3 ft. long by 1 ft. thick, was brought to the Botanic Gardens, stood in a shady place and well watered every day: it is now two years since the study began and the log still bears abundant fruit bodies in wet weather. Petch considers that *C. apalosarca* may be parasitic, but I have seen no evidence of this in Malaya, and from Fischer's work it is doubtful even if *Armillaria mucida* is a true parasite.

The material of *Collybia radicata* was gathered scantily in Singapore and Pahang, and at Brastagi in Sumatra. It occurs in the lowland and mountain forest but is rather scarce, and the fruit bodies never form troops on cut stumps as in Europe; they grow singly, or two or three together, from dead roots and appear to be humicolous.

#### DESCRIPTION

##### *Collybia apalosarca* B. & Br.

Pileus 4 mm.-15 cm. wide, convex then *plane*, often gibbous, never revolute, sometimes rugulose, with a smoky viscid gelatinous pellicle often spotted with greyish flecks, striate in small specimens, dark umber becoming paler fuscous brown and finally dirty white when old, rarely pallid white from the first; margin slightly incurved at first, thin, acute, entire.

Stem 3 mm.-9 cm. long by 0.5-9 mm. wide at the apex, 1-14 mm. at the base, gradually tapered upward or subcylindric, central or

slightly excentric, straight or incurved; base dilated, discoid, mostly with a narrow ridge or zone round the distal margin as the trace of the ring; solid, fibrous; attached by a microscopic root; thinly white villous below the ring; above the ring, pruinose or subvillous, white or pale clear yellow when young, sometimes with pale rufescent streaks; apex often subcostate.

Veil very thin, evanescent.

Gills rounded adnate, adnexed or almost free, often separating free, sometimes with a subdecurrent tooth, more or less ventricose, rather crowded, broad, rather thick, waxy, submucilaginous, not veined, 1-5 ranks with 11-39 primaries, 1-12 mm. wide, white, often with the edge pale clear yellow at first, becoming powdered with the spores and brownish in decay.

Flesh fairly thick, subhygrophanous, rather brittle, 0.5-5 mm. thick in the centre, 0.3-3 mm. thick half-way to the margin, white, with a thick gelatinous layer, 0.3-1 mm. thick on the surface of the unexpanded pileus.

Smell of fresh fish, sometimes strong.

Spores 16-23  $\times$  16-22  $\mu$ , white, subglobose to broadly ellipsoid, with a small apiculus, smooth, with the wall thickened about 0.5  $\mu$ , densely granular-guttulate with fine oil-drops.

Basidia 54-75  $\times$  18-25  $\mu$ , large, subclavate, monomorphic, densely multiguttulate as the spores, with four stout subarcuate sterigmata 5-9  $\mu$  long  $\times$  3.5-5  $\mu$  wide at the base.

Cheilocystidia forming a sterile edge to the gill, clavate, rarely subventricose, often with a long stalk thin-walled, colourless, vacuolate, 45-95  $\times$  8-28  $\mu$ , mostly 10-15  $\mu$ , and 2.5-4  $\mu$  at the base.

Pleurocystidia 110  $\mu$ -280  $\times$  23-40  $\mu$  in the middle, 10-16  $\mu$  at the apex and 3-4.5  $\mu$  at the base, very large, broadly fusiform with rounded apex or ventricose with the apex prolonged and subcylindric, with a long thin stalk, colourless, vacuolate, thin-walled.

**f. radicans f.nov.**

Stipes radicans, e rhizomorpho longo evolutus.

A modification with a "rooting base"; common with the typical form.

**var. *perstipitata* var.nov.**

Stipes ex integro elongatus, velo universalis a basi usque ad medium tenuiter tunicatus disco basali deficiente.

The stem elongating from the base, without a disc, thinly sheathed with the veil which ends in an indistinct zone about the middle; of small size, the pileus not exceeding 5 cm. wide and the stem 6 cm. long. Much less common than the typical form.

## THE STRUCTURE OF THE MATURE FRUIT BODY

The microscopic structure is complicated. Almost every apical cell on cessation of growth enlarges into a basidium or a cystidium, these varying in size and shape in different parts of the fruit body, and forming a palisade at every external and internal surface. Fig. 1 is a diagram of the structure of a primordium in which the marginal

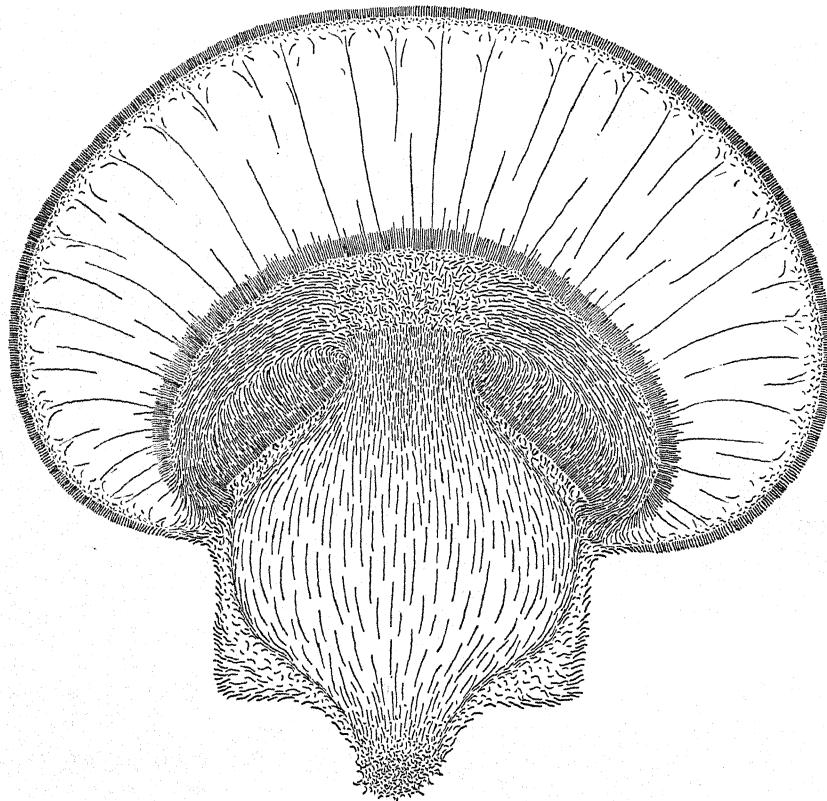


Fig. 1. A diagram of the structure of a primordium about 6 mm. high, in which apical growth of the parts has finished.

growth of the pileus and the down-growth of the gills have been completed: all parts of the fruit body are thus defined and need but to expand by sympodial branching and inflation of the cells to their full size. Immediately above the point of emergence of the stem from the wood there is a bulbous base which will become the disc. The shank of the stem is confined in a short, rapidly tapering frustum of a cone and is surrounded by the pileus, whose margin is attached by the

veil to the edge of the disc. A thick gelatinous blanket envelopes the pileus. The gills almost fully occupy the gill cavity.

A loose palisade forms a thin villous layer round the sides of the disc. It is continuous with the *external* palisade of the pileus, which together with its thin interwoven hypoderm forms a superficial elastic pellicle holding the jelly in place. Another loose palisade covers the supra-annular portion of the stem. Along the edges of the gills and at the margin of the pileus there is a close palisade of sterile cells which differ in shape from the cystidia in the hymenium, and at the boundary between the jelly and the firm flesh of the pileus there is the *internal* palisade of the pileus.

For convenience in description, I have followed Buller's method of naming the sterile apical cells of the fruit body (6). Those on the surface of the pileus are *pileocystidia*, those on the stem are *caulocystidia*, those on the sides of the gills are *pleurocystidia* and those on the gill edges are *cheilocystidia*.

The detailed structure of the parts is as follows:

**The stem.** The medullary hyphae in the elongating part of the stem are colourless, thin-walled, strictly longitudinal and compact. In the middle portion, between the disc and the stem apex, the cells are  $100-800 \times 8-30 \mu$ , mostly  $12-20 \mu$ , but a few are uninflated, only  $3-5 \mu$  wide, and are passively drawn out to various lengths. At the apex of the stem the cells are as wide but shorter,  $50-200 \mu$  long. At the base of the stem and in the disc they are  $5-12 \mu$  wide and too much interwoven for their lengths to be measured. In the plug, which fixes the fruit body to the wood, the hyphae are not inflated; they are  $3-5 \mu$  wide, very closely interwoven, without air spaces between them, and with firm, slightly thickened walls; they thus form a strong tough rope-like tissue.

The palisade on the disc is composed of thin-walled, colourless hyphae,  $3-5 \mu$  wide, loosely interwoven and directed obliquely outwards. Their terminal cells are slightly inflated,  $5-8 \mu$  wide, and sub-clavate or subventricose, with clear vacuolate contents; the walls may be smooth or thinly encrusted in places with minute yellowish granules.

The outer medullary hyphae in the supra-annular portion are narrow,  $2-6 \mu$  wide, and bear superficial branches which project more or less obliquely outwards to form the loose palisade, macroscopically the pruinosity. This palisade is best developed in the proximal half of the stem and is absent from the extreme apex, which macroscopically is glabrous. The palisade is formed from laterals which grow out into the gill cavity in the primordium; at the apex the gills are pressed so tightly against the stem that not a single cell can be extruded. In the proximal half, the hyphae of the palisade are composed of two or three cells, each  $40-90 \mu$  long, and the palisade is rather denser than on the disc. Towards the apex of the stem, the

hyphae are shorter and reduced to single cells. The terminal cells are inflated,  $6-17\ \mu$  wide, and are ventricose, subfusiform or clavate, thin-walled and colourless; their contents are either widely vacuolate or rather vitreous and smeary-looking with few vacuoles, or wholly clouded with very fine vacuoles and minutely reticulate. The sub-terminal cells are either cylindric,  $3-5\ \mu$  wide, or also more or less swollen, up to  $15\ \mu$  wide, and with similar contents. On the elongation of the stem the palisade is more or less disrupted and the pruinitis may tend to become a minute scurfiness.

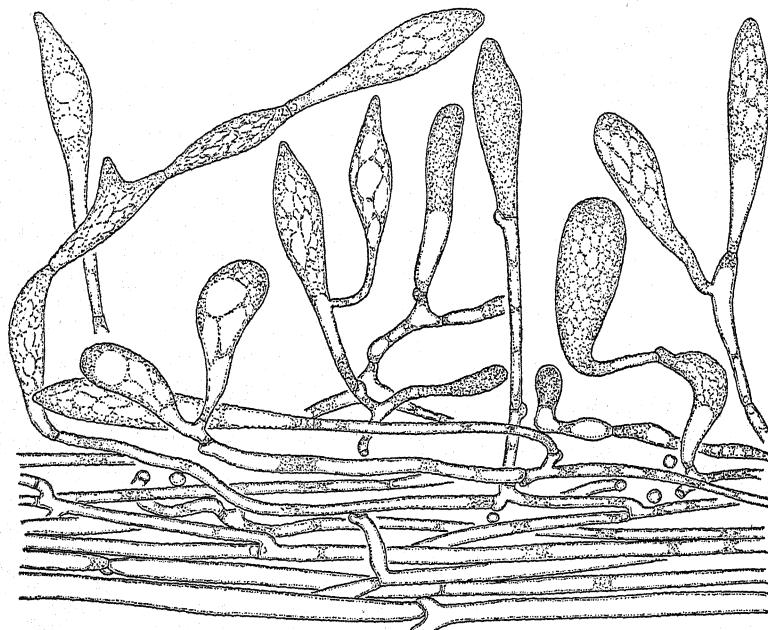


Fig. 2. A part of the palisade from the middle of the stem of *Collybia apalosarca*:  $\times 500$ .

Among these superficial hyphae are numerous yellowish, oily-looking blobs and granular masses which may be derived from the breakdown of some of the hyphae, or may be exudates. When abundant they cause the clear yellowish tinge often seen on the stem of fresh specimens. They sometimes occur on the gill edges and impart to them the same colour.

A secondary mycelium is absent.

**The pileus.** The hyphae are interwoven in the centre, immediately above the stem, and longitudinal in the limb. They have thin colourless walls and are widely vacuolate. The cells are  $60-500 \times 8-30\ \mu$ , though a few may be narrow,  $3-5\ \mu$ , and passively drawn out as in the

stem. Air spaces occur between the hyphae, which have dry walls, except over the gills and in the trama, where the spaces between the hyphae are reduced and filled apparently with free water.

The internal palisade is formed of narrow hyphae directed perpendicularly into the jelly from the surface of the pileus, as shown in Fig. 3. It is about  $100\mu$  high. The hyphae are  $2-3.5\mu$  wide, in places swollen to  $6\mu$ ; they have short cells,  $25-50\mu$  long, which are

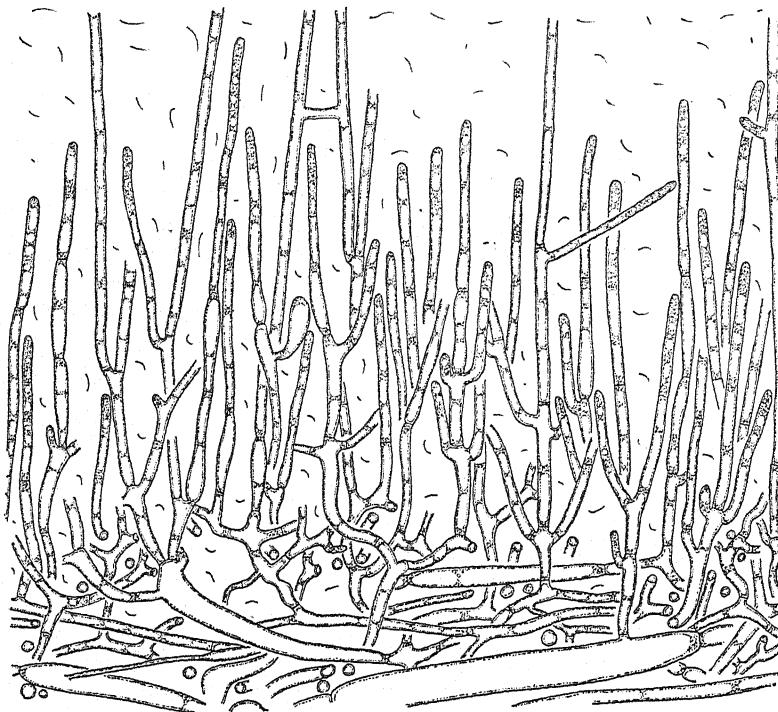


Fig. 3. A part of the internal palisade from the centre of the pileus of *Collybia apalosarca*:  $\times 500$ .

frequently branched, one to four branches arising near the distal end of each, and they terminate in simply rounded apices. Their cell contents are vacuolate with a pale fuscous or pale umber pigment in the cell sap.

Immediately below the internal palisade there is a narrow hypoderm,  $30-40\mu$  thick, of rather closely interwoven, narrow hyphae,  $2-5\mu$  wide, also with the pale umber pigment in the cell sap. It is these hyphae which have given rise to the palisade and they are intricately entangled, becoming stretched and distorted when the pileus expands.

The jelly is traversed perpendicularly to the surface of the pileus, by rather scattered, fine, colourless hyphae,  $1.5-2.5\mu$  wide, the cells of which are  $50-150\mu$  long and have tenuous mucilaginous walls. They issue from the flesh of the pileus; most of them pass through to the external palisade, forming tufts of pileocystidia, but others end



Fig. 4. A part of the external palisade from the centre of the pileus of *Collybia apalosarca*:  
 $\times 500$ .

blindly in the jelly and represent hyphae of the internal palisade which have grown out beyond the general level. The thickness of the jelly varies with the amount of water available; in wet weather, it may reach  $2.5$  mm. thick in the primordium. On expansion of the pileus it is stretched and slithers off, and in dry weather it is thin and rubbery.

The external palisade is formed from the terminal cells of the hyphae which traverse the jelly (Fig. 4). These pileocystidia are very variable in shape and size. They are ventricose, flask-shaped or sub-cylindric, rarely clavate, often flexuous,  $70-200 \times 6-11 \mu$ , with vacuolate contents and mostly with the pale umber pigment in the cell sap. Beneath the palisade there is a hypoderm of rather closely interwoven hyphae which have arisen as branches from the subterminal cells, and their terminal cells contribute also to the palisade: the cells of this layer are mostly  $35-200 \mu \times 2-5 \mu$  but they may be inflated up to  $12 \mu$  wide, and, as in the hypoderm of the internal palisade, they are pulled out and distorted on expansion of the pileus. The palisade is at first fairly compact, but, as the primordium enlarges, it is stretched also and the pileocystidia are pulled apart and come to lie in any direction; finally, on full expansion, the pellicle is torn into small pieces which persist as grey flecks or are washed off by the rain.

**The gills.** The trama is composed of longitudinal, fairly compact hyphae similar to those of the pileus. (By longitudinal in the gills is meant in the direction of marginal growth, which is normal to the limb of the pileus.) The hyphae in the subhymenium are closely and intricately interwoven: they have slightly mucilaginous walls and their cells are short and narrow,  $10-25 \times 3-6 \mu$ , though occasionally  $12 \mu$  wide.

All the hyphae of the fruit body have a clamp at each septum except those of the internal and external palisades with their hypoderms and those which traverse the jelly; they are not clamped.

#### THE MACROSCOPIC DEVELOPMENT OF THE FRUIT BODY

I observed carefully the development of fifty-one fruit bodies. For twenty-one of these I was able to record the rate of growth from the first white flecks visible to the naked eye to the collapse and decay: for the rest, the observations cover only the later stages from expansion to collapse.

On the large log of *Araucaria*, fruit bodies of all sizes developed, from those with mature pilei only 4 mm. wide to others with the pilei 14 cm. wide: but from smaller bits of wood, 8-12 in. long  $\times$  3-4 in. thick and wide, and on bits of bark, only small fruit bodies were obtained, none of which had pilei larger than 5 cm. wide. For the production of large fruit bodies it thus appears that the mycelium requires a large piece of wood to grow in.

The primordia are mostly solitary. When two or three are formed close together one usually takes the lead at an early stage and the others abort or develop into stunted specimens. Once, however, a tuft of six almost equally developed fruit bodies with pilei 6 cm. wide was produced from the large log, and tufts of three to five large indi-

viduals are occasionally found in the forest. Sometimes also, for no apparent reason, the primordia develop normally for two to three days, then stop, shrivel and rot away: a great many of my observations were nullified in this way.

When the hyphae grow out from the bare wood or from the surface of bark, they develop straightway into the primordium which is thus attached only by a microscopic "plug" to the mycelium. But if they arise under the bark or in a deep crack, they then grow out into a long cylindrical or flattened white strand, 1-2 mm. thick. While it is confined the apex of the strand is conical, but on reaching an opening, or on being acted upon by light of sufficient intensity, it dilates into the primordium. Such fruit bodies have thus a distinct "root" of varying length. The "root" is homologous with that of *Collybia radicata*. It should be regarded as a short rhizomorph.

For convenience, the fruit bodies which I studied can be divided into four groups, namely large ones with the mature pileus 6-11 cm. wide, medium-sized ones with the pileus 2-5 cm. wide, small ones with the pileus less than 2 cm. wide, and perstipitate ones in which the pileus did not exceed 4 cm. wide. Most observations were made on medium-sized ones. The primordia were always superficial and development was straightforward.

The primordia are first visible as minute white flecks about  $100\mu$  high, which can scarcely be more than a few hours old; they develop at any time of the day. In twenty-four hours they are about 1 mm. high and the pileus has just begun to form. The apex of the primordium is rounded and slightly greyish, since the hyphae of the veil above the pileus have already begun to gelatinise. During the next fifty hours or so, the primordium gradually develops into a sessile, or shortly stalked, dark brown hemispherical body about 6 mm. high. In this state it corresponds in structure with the diagram in Fig. 1: the tissues of the stem, pileus and gills are completed, and on inflation of the cells and development of the spores the fruit body will become mature. The brown colour of the upper surface begins to develop when the primordium is only thirty-six hours old, and it is due to the appearance of the pale umber pigment in the palisades of the pileus. The rest of the primordium is seen in section to be white, though sometimes the surface of the stem and the edges of the gills are yellow from the granular matter deposited on them.

Having developed thus far, the primordium expands on the following night and by next morning the pileus is about half-open. It remains like this during the daytime and on the next night it expands fully, the limb becoming plane. The fruit body then persists in this state for another thirty-six hours or so. On the first night, expansion does not begin until after dusk and is probably not appreciable before 9-10 p.m. Elongation begins in the stem just above the disc and pro-

ceeds thence acropetally to the apex and centrifugally along the limb and down the gills. The limb rises both through the inflation and straightening of its own hyphae and through the upthrust of the gills. And if, as usually happens, the primordium has developed from an oblique or vertical surface, it is during this first night of expansion that the pileus is set so that the longitudinal axes of the gills are brought vertical and both sides of the gill face obliquely downwards. The adjustment is brought about by a curvature of the stem apex, the cells on the under side elongating more than those on the upper side: for, it will be remembered, the cells in this part are not fully extended and thus have a reserve to effect such alterations.

The veil is ruptured during the first night in the early hours of the morning; as the hyphae in the stem and the centre of the pileus elongate, the limb is forced upward and outward and the margin breaks away from the disc leaving the narrow ridge round its margin as the trace of the ring (inferior annulus). The grey pellicle on the pileus is split up into irregular patches and the jelly, thus freed, slithers over the surface and drips from the edge or, if the veil clings more firmly on one side of the disc, the jelly is drawn over from the opposite edge of the pileus and collects in a sloppy mass round the stem.

The first spores are shed a little before the rupture of the veil so that they are not properly dispersed. In a few hours, by sunrise, sporing is copious and lasts until the collapse of the fruit body.

The gills generally collapse first owing to the numbers of bacteria which develop among the effete basidia. Then the pileus follows in a few hours, hanging limply round the stem. But the base of the stem and the disc are firmer, their hyphae having slightly thickened walls, and they persist as unsightly relics for several days. The hyphae can maintain their turgidity only for a few days.

The primordia are not attacked by beetles, but small flies lay their eggs on the gills and their minute maggots browse on the hymenium, just as in *Collybia radicata*. Snails devour the fruit bodies at any stage and special measures had to be taken against them.

So, of the six and a half days which are the span of life of a medium-sized fruit body, three and a half are spent in developing a hemispherical primordium. Expansion is accomplished in the ensuing twelve hours of darkness on the fourth night and sporing lasts for a little over two days.

The procedure in small fruit bodies is almost the same. The development of the primordium takes some twelve hours less, but they expand on the fourth night. The pileus is always fully open by the next morning, and thus the fruit body lasts longer, for about fifty hours, in the mature state.

The primordia of large fruit bodies take nearly a whole extra day in

developing, thus reaching a larger size, and they do not expand until the fifth night. As with the medium-sized fruit bodies, the pileus is only half-open on the next morning and flattens out on the following night. The fruit body also lasts for a third day after expansion and persists in the mature state for about sixty hours. The span of life of large fruit bodies is therefore eight and a half days and they spore for a little over three days.

The development of the perstipitate variety is intermediate in character. It also does not expand until the fifth night, taking four to four and a half days for the development of the primordium, but it lasts only for two days after expansion like the medium-sized fruit bodies. The pileus may be fully open by the morning following expansion, as with small fruit bodies, or not until the second morning as with medium-sized and large fruit bodies: and this regardless of size. The process of expansion is also rather different, being less confined temporally as well as spatially. The elongation of the stem proceeds acropetally from the very start; the primordium of the pileus is projected farther and farther from the substratum. The part which elongates in this stage is the infra-annular portion of the stem, equivalent to the disc in the typical form, but the parts which elongate on the night of expansion are the supra-annular portion, the pileus and the gills, just as in the typical form. It will be shown presently, that even in the typical form the cells begin to elongate in the stem before the pileus is completed and the resulting increase in height of the primordium accommodates the limb and the gills in their down-growth, but this primordial expansion is macroscopically insignificant compared with that which takes place on the opening of the mechanism.

Perstipitate fruit bodies with relatively slight elongation of the infra-annular portion of the stem are usually as firm and stable on expansion as the typical form, but those with a long infra-annular portion are very insecure, especially when growing from a vertical surface. They have no supporting disc, and as the pileus expands the stem sags lower and lower, necessitating greater and greater curvature of the apex to set the limb and increasing the moment of the pileus about the origin of the stem. Finally, the fruit body usually spins round and hangs upside down in a most impracticable manner. To ensure normal development, I was obliged to prop them up with pieces of wood on the afternoon before expansion.

The data on development are arranged in Table I and schematised in Figs. 5 and 6. The period of development covers the interval from inception of the primordium to the flattening of the pileus; the period of maturity extends from the end of development to the collapse of the fruit body. It must not be supposed that the time intervals will always apply rigidly, but they give a fairly accurate idea of the life of fruit bodies of different sizes. On the whole the larger the fruit body

the longer the periods of development and sporing, but between the largest and the smallest there is little difference. The smallest had a mature pileus only 4 mm. wide and stem 3 mm. long, so that in linear measure it was about one-twentieth of the size of the largest (pileus 11 cm., stem 4.5 cm.) which I observed develop: yet, its period of development was 82 hours, and that of sporing 52 hours, compared with 116 hours and 76 hours respectively for the large one. This small specimen had the shortest life (134 hours) which I observed. But another small specimen (pileus 6 mm.) lasted in the mature state

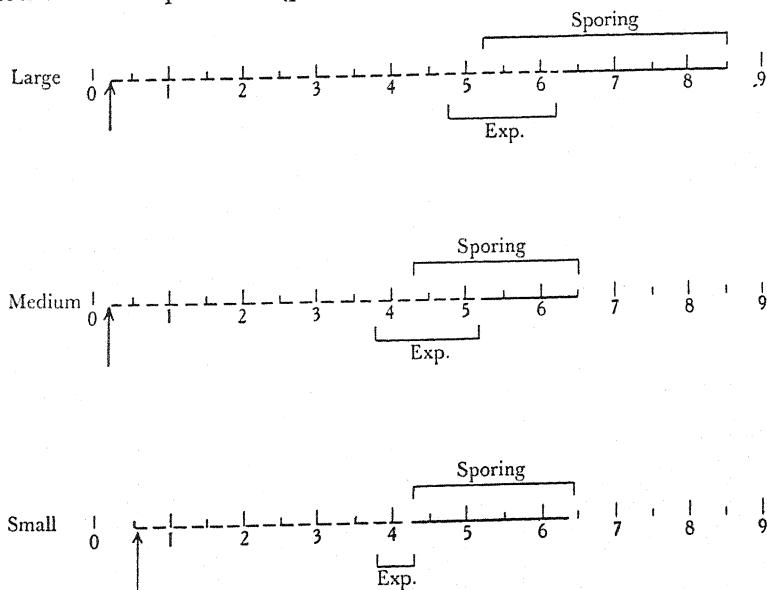


Fig. 5. A scheme of the life histories of large, medium-sized, and small fruit bodies: the periods starting from midnight (0 hours 0 days) at the origin: the figures marking intervals of twenty-four hours (12 a.m. on successive nights) with the points of midday indicated by short vertical dashes: the broken line covering the period of development from inception at the arrow: the continuous line covering the period of maturity: exp. the period of expansion.

nearly 60 hours and had a life of 152 hours, which is as long as that of medium-sized fruit bodies. The longest life was that of a large specimen (pileus 8 cm.) which expanded, as usual, on the fifth night but lasted an extra day in the mature state, thus having a life of nine and a half days, a sporing period of four and a half days and a period of maturity of more than three days. The shortest period of sporing (barely 48 hours) and the shortest period of maturity (26 hours) was observed in a medium-sized fruit body (pileus 3 cm.) which was not fully expanded till after the fifth night; it had a life of just over six days.

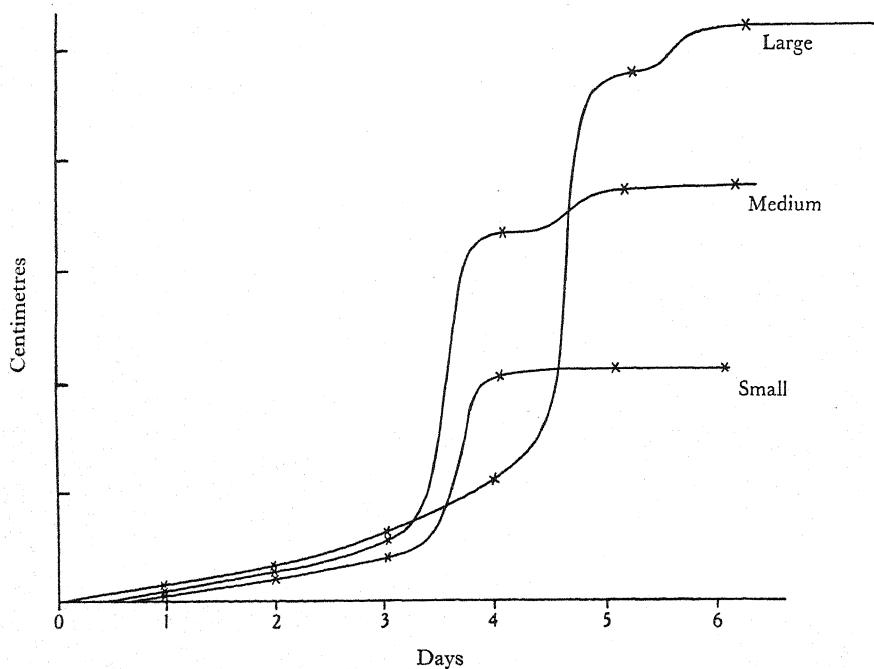


Fig. 6. A graph showing the rate of growth of large, medium-sized, and small fruit bodies: the heights of the fruit body as ordinates, the intervals of time as abscissae: the readings taken at 8 a.m. on successive days.

Table I

	Width of mature pileus	Size of primordium on the afternoon before expansion	Life	Period of development	Time at which expansion begins	Period of sporing	Period of maturity
Large fruit bodies	60-110	12 high $\times$ 10 wide	200	140	110th	78	60
Medium-sized fruit bodies	20-50	6 high $\times$ 5 wide	152	116	88th	54	36
Small fruit bodies	below 20	1.5-4 high $\times$ 1.5-3 wide	142	90	80th	54	52
Perstipitate fruit bodies	18-37	Stem 25-35 high Pileus 4-12 wide	144-168	108-120	96th-108th	46-54	36-4

Time in hours. Size in millimetres.

72 hours = 3 days, 96 = 4 days, 120 = 5 days, 144 = 6 days, 168 = 7 days, 192 = 8 days, 216 = 9 days.

I found no indication how the primordia are timed to expand during the night. No primordia ever expanded during the daytime though they began to develop at any hour. The time when expansion starts varies slightly because the pilei of similar fruit bodies may be a third, a half or two-thirds open on the following morning. With primordia developed naturally, one might expect a process requiring so much water to take place at night when the air is saturated and dew is forming, but I grew fruit bodies under a bell-jar in an atmosphere continuously saturated and others under a dripping tap with a film of water flowing over the wood, and expansion occurred only at night. The humidity of the air cannot therefore be a primary factor and one must suppose that the process is conditioned by temperature or light, and that the primordia on reaching a certain stage in development become sensitive to this stimulus which arises at nightfall. It may be remarked here that Morquer found in *A. mucida* that abundant moisture was required for complete fructification and that fruit bodies grown in the dark were abnormal and sterile<sup>(17)</sup>: yet Fischer raised fruit bodies of the same species in darkness which were normal except for the lack of pigment.

(My observations were made at sea-level in the tropics; the temperature averaged 80° F.,  $\pm 8^\circ$ , with sunrise and sunset about 6 a.m. and 6 p.m.)

#### THE MICROSCOPIC DEVELOPMENT OF THE FRUIT BODY

I have not worked out the hyphal system of the fruit bodies in detail, for the jelly on the primordium renders them difficult objects to handle and section, and one must use fresh material. But the origin of the different tissues and palisades is quite clear.

**The primordial shaft.** Before the pileus develops the subcylindric or subconical primordium is composed of hyphae directed more or less longitudinally, though they are closely entwined, and the apical growth of the hyphae at the distal extremity causes the apical growth of the primordium. The direction of apical growth is probably determined by a positive phototropism and thus the longitudinal arrangement of the hyphae, while the extent of apical growth, as already mentioned, may be determined by the intensity of light falling on the apex. The hyphae at the apex grow and branch monopodially: they are narrow,  $2-3\mu$  wide, and the cells which they cut off are  $8-16\mu$  long. The growth of the hyphae round the periphery of the apex slackens off and their terminal cells enlarge to  $5-8\mu$  wide, becoming subclavate or subventricose as the distal or proximal part is most distended: their ends point obliquely outwards and from the subterminal cells short laterals, of few cells, may arise and the terminal cells of these are similarly arrested and inflated about the same level. The primordial shaft is thus thinly corticated with a loose palisade,

which becomes the palisade of the disc, or of the infra-annular portion of the stem in the perstipitate variety. The older cells composing the body of the internal tissue begin slowly to enlarge acropetally from the attachment plug, from a very early stage. The structure of such a primordium before apical growth is arrested is shown in Fig. 7 *a*; the cells in the lower part would already be  $25-40 \times 5-7 \mu$ .

The pileus is initiated not by the arrest of apical growth of the primordial shaft but by an increased branching of the hyphae in the interior shortly below its apex. The laterals arise mostly from the central longitudinal hyphae about  $100 \mu$  below their apices, and they grow out in all directions between the other longitudinal hyphae, surrounding them or pushing them aside; they branch profusely themselves and from a very compact subglobose mass of plectenchyma visible to the naked eye as a slight swelling. Within a few hours, the laterals on the proximal side of the swelling come into alignment as the growing margin of the pileus and proceed to build the limb; such a stage is shown in Fig. 7 *b*. Now, theoretically, the pileus is never exposed. Over its centre are the parts of the longitudinal hyphae distal to the regions where they gave off the laterals which build the limb, and these parts continue to grow apically for a considerable time longer: and on the outside of the incipient limb are the longitudinal hyphae which were pushed aside by the laterals, and also several hyphae which for some reason are stimulated to grow up from the cortex of the primordial shaft immediately below the incipient limb, and together these hyphae form a loose sheath round the margin. It is as if the head of the primordium were covered with hair from the first and its sides were surrounded by a high cravat, but, as this cravat is only one or two hyphae thick and as the hyphae are often loosely arranged, for such purposes as respiration and evaporation the margin of the pileus is practically exposed.

The hyphae at the margin of the pileus branch monopodially. They grow obliquely, outward from the apex of the stem and downward towards the base, so that the limb becomes deconic, but eventually they are directed more or less perpendicularly toward the surface of the stem and the extreme margin of the pileus is therefore slightly incurved, as in Fig. 7 *c*, and in Fig. 1. It is difficult to decide whether the curvature is brought about by a directional growth of the hyphae or is merely a mechanical effect of the very considerable multiplication of hyphae going on over the surface of the pileus at the same time, which tends to force the limb downward on to the stem in much the same way that the development of the cortex in the apothecium of Discomycetes forces the margin upward and inward.

While the margin of the pileus grows as a very compact ridge within the tenuous sheath surrounding it, many hyphae grow out from the upper surface of the limb just behind the margin and interweave with

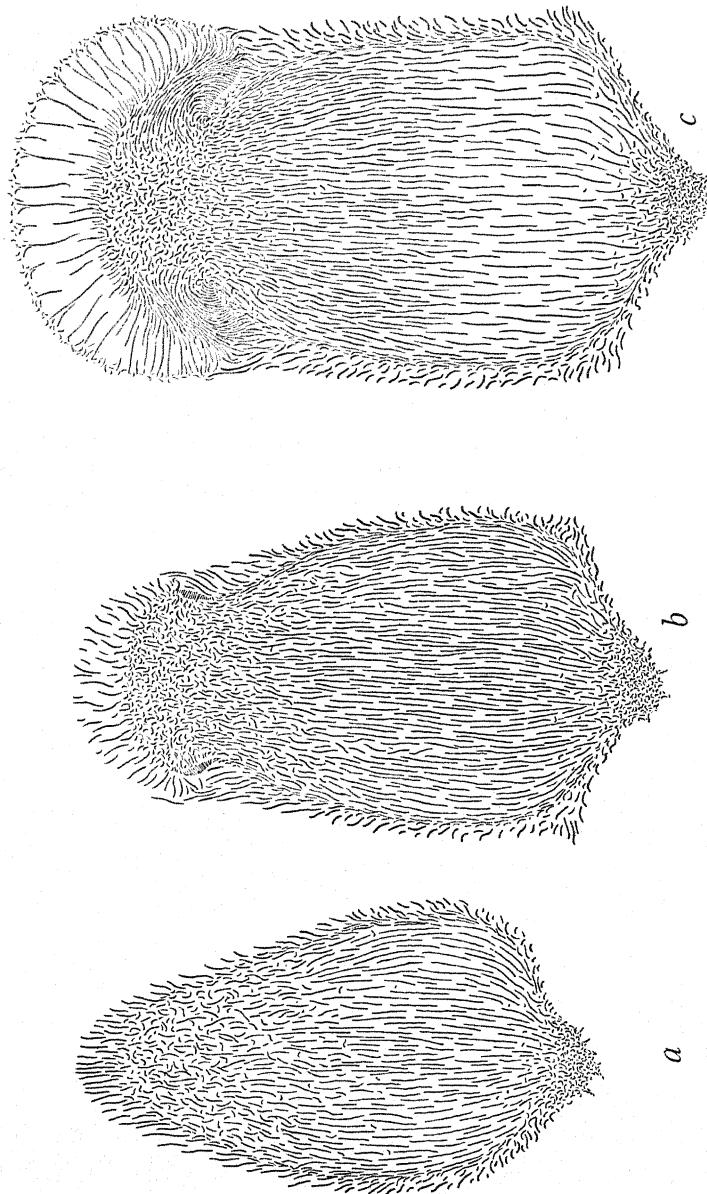


Fig. 7. Diagrams of the early structure of the primordium: *a*, the primordial shaft; *b*, with the limb just forming; *c*, with the palisades, the gelatinous layer, the limb and the gill cavity established.

those of the sheath which, as already mentioned, have grown up from the loose palisade of the primordial shaft. In reciprocal manner more hyphae grow out from the surface of the stem near to the margin and interweave with those excrescent from the pileus. Thus an anastomosis between the loose palisade on the pileus and that on the stem takes place at the margin of the pileus at an early stage, some twelve hours after the inception of the limb, and the conjoint tissue forms the marginal veil. It is thin and rather scanty yet strong enough to hold the margin of the pileus until the night of expansion. Consequently, as the pileus increases in size by marginal and intercalary growth, the limb arches upward and outward and the narrow space between it and the stem is enlarged into the gill cavity.

Meanwhile, the ends of the original longitudinal hyphae at the apex of the primordium continue to grow out beyond the pileus. They branch frequently and they are joined by other narrow hyphae excrescent from the limb. At an early stage, so soon even as the pileus is started or shortly after, the walls of these hyphae become mucilaginous and the pale umber pigment appears in their cell sap, and so long as the margin of the pileus grows it gives off similar excrescent hyphae, some of which, as just described, contribute to the marginal veil. When the pileus is 0.5-1 mm. high, the outgrowth of these hyphae is arrested; their apices turn aside and interweave a little before the terminal cell enlarges and becomes subclavate or subventricose. Much sympodial branching then occurs from their sub-terminal cells: the laterals consist of a few cells only and in turn their apical growth is arrested and their terminal cells enlarge. Thus the primordial pileus becomes covered with a convex pad of gelatinous tissue bounded at the free surface by a palisade of subclavate or subventricose cells: these cells gradually elongate and the layer forms the external palisade of the pileus; it is incipient in Fig. 7 c.

During the period of intercalary growth of the pileus, which lasts until the final stage of expansion, narrow hyphae,  $2-3\ \mu$  wide, continue to grow out into the jelly from the surface of the limb. Some reach the external palisade where they form pileocystidia, but most, and in later stages probably all of them, do not reach a greater length than  $100\ \mu$  before their apical growth is arrested, when they branch sympodially from the proximal cells and the laterals grow up more or less parallel with the parent hyphae to the same level or are stopped at shorter distances. Thus is constructed the internal palisade of the pileus.

The jelly imbibes the drops of rain and dew which settle on the pileus. It swells and stretches the external palisade, despite the inflation of its cells, and the primary hyphae traversing the jelly are pulled out and become tenuous and not more than  $1-2\ \mu$  wide in the mature tissue. The dome of jelly acts as a resilient buffer and as a screen against evaporation; one might almost call it amniotic.

**The gills.** The gills arise on the proximal side of the limb as ridges radiating from the apex of the stem. The primary gills are started shortly after the limb itself and in such a stage as Fig. 7 c they would already be visible as slight flutings: according as they start some distance down the stem or from the extreme apex so they are adnate, adnexed or nearly free in the mature fruit body. As they proceed radially following the limb, they diverge and at a certain distance apart the secondary gills are started in the widening intervals: after the gills have again diverged to the same extent the tertiaries are started and finally, in large pilei, quaternaries may be intercalated. The gills do not reach the extreme margin of the limb; there is a smooth narrow zone at the periphery, corresponding to the pore field in polypores, to the proximal border of which the gills can be traced. The slit between the limb and the stem, into which the gills project, is at first more or less open to the exterior, being loosely fenced round by the hyphae of the sheath: on the development of the veil it is closed into an annular cavity. The cavity enlarges through the arching of the limb but the gills grow so rapidly that it never appears as more than a slit in radial section, and eventually the edges of the gills are pressed against the stem on to which they imprint faint longitudinal striations.

In such a stage as Fig. 7 c, the under side of the limb, bordering the gill cavity, consists of a very compact palisade of down-growing hyphal ends,  $3-5\mu$  wide, which extends from the stem apex to the margin. Apical growth is most rapid at the margin where the tissue of the limb is being formed. In the smooth narrow zone corresponding to the pore field, apical growth slackens and eventually stops, whereon the hymenium is constructed by sympodial branching. But along the lines of the gills outgrowth is stimulated afresh: linear radial growing regions are formed similar to that at the margin, and they are the edges of the gills. Along the edges of the young gills there is certainly an apical growth of the hyphae by which they are built out into the gill cavity, the proximal parts of the hyphae forming the trama of the gill. But I was unable to determine the exact manner of growth. The hyphae may be persistently monopodial or, as it sometimes seemed, they may form a kind of sympodium in which apical growth slows down after a few cells have been cut off and then a lateral grows up vigorously and pushes the original apex aside. Just as at the margin of the limb, however, apical growth slows down on either side of the growing region. The hyphal ends on the flanks of the gills are pushed aside by the upgrowing laterals and they come to point at right angles to their original direction, perpendicularly to the longitudinal hyphae in the trama. They then construct the hymenium. They cut off two or three short cells, after which the terminal cell becomes a basidium. The subterminal cells put out laterals which

grow directly or by devious routes between the primary hyphal ends and finally range themselves alongside after cutting off a few short cells; the terminal cell of the lateral then enlarges into a basidium and the subterminal cells branch in their turn. The terminal cells thus form the palisade of basidia and the subterminal cells form the subhymenium. The pleurocystidia also represent modified hyphal ends displaced from the gill edge, but in their case the terminal cells fail to cut off subhymenial cells but elongate directly into pleurocystidia: in sections of mature gills, therefore, the pleurocystidia are seen to arise from the trama and to pass through the subhymenium by means of a long stalk.

The cheilocystidia do not develop until the apical growth of the hyphae along the gill edge has been completed. The terminal cells of the hyphae then enlarge and become clavate, and, by branching from the subterminal cells, other cheilocystidia are intercalated in the same manner as the basidia on the sides of the gills. A wide compact sterile edge is thus formed.

Until the night of expansion, the basidia remain immature with clear, partly vacuolate contents. During that night they become densely and coarsely granular from minute oil drops formed throughout the cytoplasm. By 6 a.m. next morning some have already matured, and in an hour sporing is copious. The primary basidia mature in an acropetal sequence which spreads rapidly in a slanting wave from the centre of the pileus to the margin and from the bases of the gills to their edges. The secondary basidia then develop and mature over the whole hymenium without grouping: in any part, widely spaced mature basidia may be seen with young basidia in all stages of development around them. As the basidia are monomorphic and the gills are aequihymeniiferous, the fruit bodies belong to Buller's *Armillaria* subtype(6).

The spores arise as small subglobose or broadly pip-shaped swellings placed rather obliquely at the ends of the sterigmata and they have a blunt apiculus which projects from their base on the adaxial side. The contents are clear or slightly cloudy at first, but when the spores are about half-grown some of the oily granular cytoplasm from the basidium flows into them and fills up the interior except for a clear thin hyaline parietal layer. When the spore is full grown the wall thickens.

The pleurocystidia develop as gradually as the basidia. They are subcylindric at first, and as they grow beyond the level of the hymenium they become pronouncedly clavate with a long stalk and are shaped exactly like the cheilocystidia. They keep this shape while slowly growing larger until the morning before the night of expansion, when they elongate further by protruding the apical part and so become ventricose. They are largest and best formed at the base of the

gills in the central part of the pileus, where they have had longest to develop. Near the edges of the gills many of them persist in stages intermediate between the clavate and the ventricose. These transitions suggest that the cheilocystidia also, which have the shape of the young pleurocystidia, would become ventricose if given long enough to develop freely: as they are the last hymenial elements to be formed, shortly before the maturing of the basidia and the expansion of the fruit body, their growth is naturally arrested.

Both kinds of cystidia have clear vacuolate contents. Of all the cells in the fruit body only the basidia and spores have the oily granular contents. The oil droplets must be the reserve form of fats transferred in soluble components from the mycelium, precipitated in the basidia and then passed into the spores, in which state they remain until resolution on germination.

**The stem.** The inception of the pileus terminates the apical growth of the stem, the subsequent increase in length of which is due to vacuolation and elongation of the cells: the length of the primordial stem cannot therefore exceed 1-2 mm. in the typical form. It thickens also by branching of the hyphae and laterals arise especially from the surface which forms the inner wall of the gill cavity. They project shortly into the cavity, but the terminal cells soon enlarge, becoming clavate or ventricose, and then, by rather infrequent sympodial branching, a loose irregular cortex is constructed similar to that on the disc. The cortex can develop only where the gills are not pressed against the stem, and so it is thickest just above the veil and reduced towards the apex. Where the margin of the pileus touches the stem, the excrescent laterals interweave with the excrescent hyphae from the pileus to strengthen the veil, but there is no anastomosis between the edges of the gills and the palisade on the stem.

During the growth of the primordium the hyphae begin to enlarge slowly. The vacuolation of the cells, as already mentioned, proceeds acropetally from the plug to the extremity of the pileus and the gills. The rate of enlargement of the cells gradually increases, reaching a maximum on the night of expansion, and then gradually declines. The extent of enlargement of the cells also increases gradually in acropetal sequence to the centre of the pileus, except for the special region of curvature at the stem apex, and declines towards the extremities. The grand period of most rapid enlargement coincides in the typical form with the expansion of the region of greatest enlargement, which includes the supra-annular portion of the stem, the centre of the pileus and the proximal parts of the gills, and thus the nocturnal opening of the fruit body. The period of both dies away gradually and the limb and the gills are strongly attenuate centrifugally. In the perstipitate variety the grand period of both processes

is more extensive and the primordium is less perfect. Even after the enlargement of the hyphae the pileus may still flatten further through the intercalary growth of the hymenium, but as the basidia develop rapidly and collapse on shedding the spores this process is not as effective as in many other toadstools, and the pileus, though often plane, is never revolute.

The enlargement of the terminal cells in the superficial palisades proceeds independently of that of the medullary hyphae of the same part. The first terminal cells to enlarge are those in the palisade on the disc. Then follow those in the external palisade of the pileus and, shortly after, the first basidia and pleurocystidia, and lastly those in the palisade on the supra-annular portion of the stem. The terminal cells in the palisades begin to enlarge many hours before the corresponding medullary hyphae. The process depends on local conditions and is not part of the general motor mechanism of the fruit body.

#### THE SIZE OF THE FRUIT BODY

Are the undersized fruit bodies, which occur in *Collybia apalosarca* and many other agarics, juvenile forms of the normal ones or are they merely less inflated? Do they consist of fewer cells, that is, or have their cells not enlarged so much? One cannot decide from macroscopic evidence because the size of the mature fruit body is determined by three distinct processes, each of which is microscopic. In the first place, the length of any part is determined by the extent of apical growth of the constituent hyphae, *i.e.* the length depends on the number of *cells* composing the constituent hyphae: this is the property which enables one to determine directly whether a fruit body is juvenile or not, since a juvenile form is one whose growth is arrested before reaching the normal limits of the species and which matures in this state. Secondly, both the length and the width of any part depend on the amount of enlargement which the cells undergo: this is the most striking property but the one with the least morphological or evolutionary significance. Thirdly, the width and, to a small extent, the length depend on the amount of intercalary growth by branching, *i.e.* on the number of *hyphae* composing the part.

The first property is very difficult, if not impossible, to measure. In an ideal primordium with indirect development, which has firstly a period solely of apical growth and then a period solely of enlargement, it should be sufficient to measure the length of any part before enlargement begins, divide by the average length of the cells, and so arrive at the number of cells in a primary longitudinal hypha and thus the extent of apical growth. But, except perhaps in the Phalloidaceae, no primordium is so perfect. It is impossible with the primordia of agarics to decide exactly when apical growth has ceased and at what

stage therefore the measurements should be taken, and there is always some enlargement proceeding acropetally from the base from the inception of the primordium: apical growth and cell enlargement coincide in some degree from the first though maximum enlargement is delayed until apical growth has ceased. (When the primordium is poorly differentiated and develops directly, as in *Cantharellus* or *Clavaria*, the two processes are concurrent for a long time until the fruit body is half-grown or more.)

But the second property can easily be investigated and it enables one to decide indirectly if the differences in size of the fruit bodies are due to early arrest of growth (juvenescence) or merely to different degrees of inflation. The average length of the cells of the motor tissue must be determined before and after enlargement. Then, for example, if two fruit bodies of different sizes have the same average enlargement, the smaller must be composed of fewer cells (deflate them and the smaller will be smaller because its hyphae have not

Table II

Fruit body	Length of stem mm.	Width of stem mm.	Average length of cells	Width of cells	Ratio of stem-lengths	Ratio of average cell-lengths
a	45	5.0	392	8-26	1	1
b	40	4.0	398	7-28	0.9	1.02
c	30	3.5	372	8-28	0.7	0.95
d	24	3.0	415	7-24	0.5	1.06
e	19	2.5	352	7-26	0.4	0.9
f	12	1.5	219	7-23	0.3	0.56
g	5.5	1.0	281	6-22	0.1	0.72

grown so much). On the other hand, if a fruit body is only half the normal size and has about half the normal average enlargement, the difference in size is merely one of inflation. Without analysis of this sort, little meaning can be attached to differences in size. No doubt, by integration, one could find an expression for the degree of enlargement of the whole fruit body, or of one part, and by dividing the mature length by the average enlargement so determine the length due to apical growth: in any part, as the stem, the gills or the limb, all the cells do not enlarge to the same extent, the proximal ones tending to enlarge more than the distal.

In Table II the results of measuring the cells in the stem of seven fruit bodies are given: three of the fruit bodies were fairly large, two of medium size, one small and one very small. Only the cells in the region of greatest enlargement were measured, that is in the medulla of the middle third of the stem in a shell extending from  $50\mu$  inside the surface to  $1000\mu$ : the average enlargement is taken from thirty measurements. The length of the stem was measured from the top of the disc to the apex and the width was measured immediately above

the disc, for the disc which scarcely elongates must be reckoned separately; the sections were mounted in water. I have assumed that the average initial length of the cells was always the same; one cannot, of course, measure them before and after expansion in the same fruit body, nor can one tell from the appearance of the primordium at the early stage when the initial lengths must be measured what its final size will be: but in many primordia I found them to be about  $12\mu$  long when first cut off from the apical cell, and this average holds widely in many Basidiomycetes.

Take, for reference, the length of the stem in the largest fruit body,  $a$ , as unity and let  $x$  be the average number of cells in each primary longitudinal hypha in its stem. Then, as the cells in the stem of the fruit bodies  $a, b, c, d, e$ , all enlarge to much the same extent each primary stem hypha in  $b, c, d, e$ , consists of  $0.9x, 0.7x, 0.5x, 0.4x$  cells respectively, and these fruit bodies can be regarded as a series of juvenile forms in which apical growth of the axis has been arrested successively at earlier stages. Fruit body  $g$  is also an exceedingly juvenile form, but its cells have enlarged only to three-quarters of the average value. Fruit body  $f$  presents the alternative possibility: it is small chiefly because its cells have enlarged only to half the average extent though it is probably juvenile also in some degree. The argument that small fruit bodies are juvenescent will be supported by other data in the next section.

The explanation thus obtained for the length of the stem will probably apply also to the pileus because there is a close relation between the length of the mature stem and the width of the mature pileus; a fruit body with a long, massive stem has generally a wide pileus and one with a short stem has a small pileus. In the development of the gills, however, the third property becomes important. The cells of the trama hyphae enlarge, too, during the expansion of the primordium, but in the mature fruit body they are pulled apart and stretched by the intercalary growth of the hymenium. This property thus prevents the simple comparison between the lengths of the trama cells and the width of the gill in fruit bodies of different sizes, for allowance must be made for differences in intercalary growth which would be exceedingly difficult to estimate. Nevertheless, the explanation given for the size of the stem and the pileus will probably apply in some degree to the gills also, so that when a fruit body has a small pileus and a short stem through juvenescence, the gills will probably be narrow for the same reason.

A variety "minor" for small fruit bodies, without other qualification, is therefore untenable in this species, because the size of the fruit body is determined by two distinct processes apart from any effects of malnutrition or excessive evaporation.

## THE ARRANGEMENT OF THE GILLS

The number of primary gills in a fruit body depends on the width of the stem apex and the number of gill ranks upon the width of the pileus. In Tables III and IV are compiled the results of counting and measuring these properties in twenty-five fruit bodies.

Fruit bodies with small pilei and narrow stems have the fewest ranks and the fewest primaries. Among the arbitrary size groups which have been made, the small fruit bodies have 1-2 or 2-3 ranks with 11-20 primaries; the medium-sized fruit bodies have 3 or 3-4 ranks with 18-25 primaries; the large fruit bodies have 3-4 or 4 ranks

Ranks of gills

1-2 or 2	Width of pileus in mm.	4	5	6	8	14	17	21
	No. of primaries	12	11	17	11	15	20	15
2-3 or 3	Width of pileus in mm.	10.5	18	18	19	20	20	22
	No. of primaries	14	19	20	19	18	13	19
3-4 or 4	Width of pileus in mm.	36	42	45	65	72	74	76
	No. of primaries	31	23	25	30	30	31	28
							32	26
								29

Table III

Width of stem apex in mm.

0.5-1	No. of primaries	11	11	12
	Width of pileus in mm.	5	8	4
1.1-1.9	No. of primaries	13	14	15
	Width of pileus in mm.	20	10.5	14
2-3	No. of primaries	18	19	19
	Width of pileus in mm.	28	19	22
4-6	No. of primaries	23	25	31
	Width of pileus in mm.	42	45	36
7-8	No. of primaries	26	28	29
	Width of pileus in mm.	89	76	93
				65
				72
				86

Table IV

with 26-32 primaries. Now this shows that fruit bodies with small pilei, and small fruit bodies generally, therefore, are juvenescent. The number of ranks is a measure of the marginal growth of the pileus. The intercalation of a new rank follows on divergence of the pre-formed gills as they grow centrifugally with the margin of the pileus. If, therefore, marginal growth is stopped prematurely, the pileus even on expansion will have but few ranks: or, other things being equal, the greater the extent of marginal growth of the pileus the greater the number of gill ranks.

There is doubtless in each species of agaric a *spacing factor* which determines the proximity and succession of the gill ridges. The factor must be a function chiefly of the thickness of the ridges, but to determine its value observations would have to be made on unexpanded primordia. The gills are started in a region without expansion and

their original arrangement may be greatly distorted in the mature fruit body owing to the unequal enlargement of the parts. It would be necessary also to determine the inclination of the limb to the stem in the primordium and the effect of incurvature of the margin in estimating the centrifugal growth of the pileus, and to determine the amount of intercalary growth in the stem, for on this depends the size of the primordial stem apex and thus the number of primaries which it can accommodate. For such a tedious investigation the material would have to be much simpler and easier to handle than the primordia of *Collybia apalosarca* and the species of *Lentinus* with coriaceous flesh suggest themselves because they are gymnocarpic with direct development.

*COLLYBIA RADICATA*

The Malayan material of this species differs macroscopically from the European and North American in the following respects:

The pileus is subhygrophanous with the surface dry and not viscid; old pilei become slightly viscid in decay.

The stem is clothed, except for the apex, with fuscous or light brown adpressed fibrils or scurfy particles, and sometimes it is adpressedly fibrillously squamulose.

The habit is solitary, rarely two to three fruit bodies together, and always terrestrial from buried roots.

These are the numerical and microscopic data so far collected for the Malayan material:

*Pileus* 1-12 cm. wide. Stem, above ground, 6-14 cm.  $\times$  3-8 mm. at the apex,  $\times$  5-16 mm. at ground-level; below ground up to 16 cm. long, tapering to a white mycelial strand, 0.5 mm., connected to the substratum. Gills in 3-5 ranks, mostly 3-4, with 13-28 primaries 4-10 mm. wide.

Spores 11.5-15.5  $\times$  11-14  $\mu$  (Pahang specimens), 15-19  $\times$  12-15  $\mu$  (Brastagi specimens); wall *ca.* 0.3  $\mu$  thick.

Basidia 58-75  $\times$  13-18  $\mu$ , with 4 sterigmata 6-10  $\times$  3-4  $\mu$  at the base, or in some fruit bodies with only two sterigmata 9-13  $\times$  4-6  $\mu$  (rarely with a small third sterigma, sterile or with an abortive spore).

Pleurocystidia 80-150  $\times$  18-38  $\mu$ , as in *C. apalosarca*, but mostly clavate-stipitate in some fruit bodies and mostly ventricose-stipitate and prolonged in others.

Cheilocystidia as in *C. apalosarca*, but many subventricose with slightly tapered apex.

The microscopic structure is similar to that of *C. apalosarca*, there being a similar formation of palisades and cystidia, but the structure of the pileus is simpler, there being no jelly or veil, and the palisade on the stem is better developed.

**The pileus.** There is a single palisade on the pileus. It has a different composition in the centre from over the limb where, as shown in Fig. 8, three elements can be distinguished. Firstly, there are long colourless thin-walled pileocystidia,  $70-180\ \mu$  long; their proximal portion,  $30-60\ \mu$  long, is usually subventricose,  $4-12\ \mu$  wide, and the free terminal portion is filiform, straight or flexuous,  $2-3.5\ \mu$



Fig. 8. A part of the palisade from the centre of the pileus of *Collybia radicata*:  $\times 500$ .

wide, and occasionally 1-septate. Secondly, there are large clavate, or subventricose, thin-walled pileocystidia,  $40-70 \times 8-20\ \mu$ , which form the body of the palisade on a level with the subventricose portions of the first elements: they appear like sterile basidia but they are simply vacuolate, not oily granular, and occasionally they contain the pale umber pigment. Thirdly, small clavate, or subcylindric, thin-walled pileocystidia,  $15-40 \times 5-12\ \mu$ , with the pale umber pigment in

their cell sap: these elements are packed between the stalks of the other two, so that the whole palisade appears to rest on a deeply pigmented layer. It seems that these three elements have developed successively by sympodial branching of the terminal hyphae. The long colourless pileocystidia are probably the first-formed elements derived from the ends of the primary hyphae of the primordial shaft on inception of the pileus. Of their laterals, some may develop similar pileocystidia but probably most develop the large clavate colourless elements. Then, in turn, these give rise to the small clavate pigmented elements, which are thus the shortest because they are the youngest.

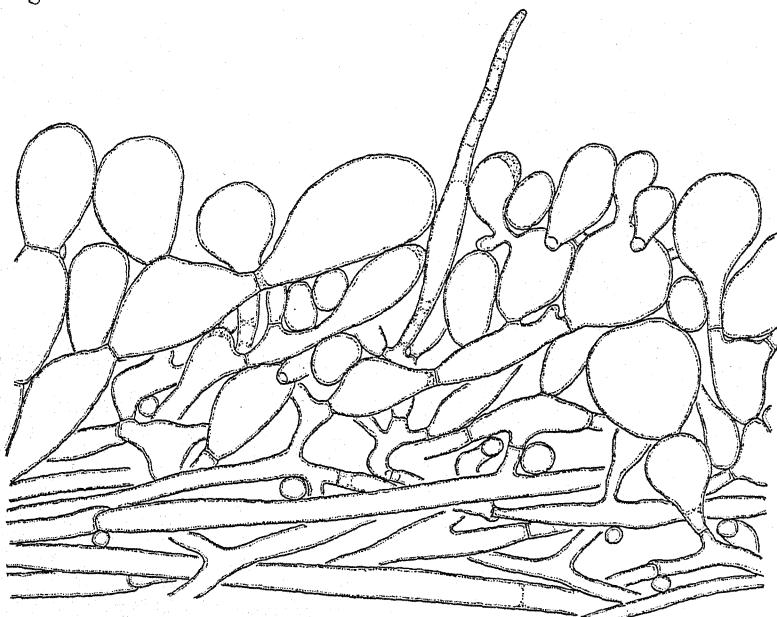


Fig. 9. A part of the palisade from the distal half of the limb of *Collybia radicata*:  $\times 500$ .

Over the limb the palisade consists almost exclusively of large clavate pileocystidia,  $25-75 \times 10-30 \mu$ , with clear umber sap (Fig. 9). Their subterminal cells are more or less inflated and pigmented and the whole forms a pseudoparenchymatous layer thinning off to the margin of the pileus, where only the terminal cells are inflated. Colourless filiform pileocystidia, like the first elements of the palisade in the centre of the pileus, occur sparsely but they are absent from the peripheral part of the limb.

The pale umber pigment causes the colour of the pileus as in *C. apalosarca*. The large size and rounded ends of the pileocystidia over the limb cause its innately pruinose appearance. The slight viscosity

of the old pilei is due to the collapse and mucification of the long colourless pileocystidia.

**The stem.** On the surface of the stem are clumps of excrescent hyphae projecting up to  $200\mu$ , as in Fig. 10. The terminal cells are inflated, clavate or subventricose,  $25-75 \times 8-25\mu$ , and the subterminal cells are also more or less inflated and sparingly branched. The cells are widely vacuolate and often contain the umber pigment. On the primordial stem there is evidently a continuous loose palisade,

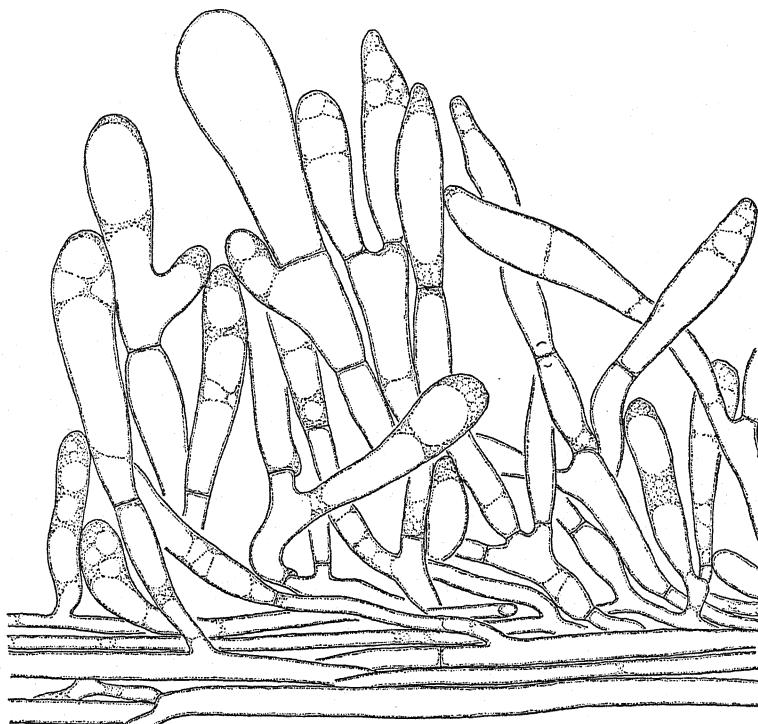


Fig. 10. A part of the palisade from the stem of *Collybia radicata*, about 1 cm. below the apex:  $\times 500$ .

which is reduced toward the apex, and on expansion it is broken up into the clumps of hyphae.

The umber pigment in the excrescent hyphae and in many of the superficial medullary hyphae causes the colour of the stem: the fibrillose and squamulose markings are caused by the disruption of the palisade.

*Collybia altissima* Massee (*Kew Bull.* 1914, p. 358), based on a collection from the Botanic Gardens, Singapore, is synonymous with *C.*

*radicata*. I have not examined the type material, if there is any, but there is a painting of the original in the Singapore Herbarium which leaves no shadow of doubt: the spore characters given by Massee are probably quite erroneous.

#### THE DATA ON *ARMILLARIA MUCIDA*

I have extracted from Fischer's papers the mycological facts germane to this study:

The spores germinate within twenty-four hours in ordinary culture media. The mycelium is white but eventually becomes orange at the base of the Petri dish; on cubes of beechwood it also becomes light orange then blood red in patches. There are no conidia in artificial culture. The air-dried spores do not retain their viability for more than six weeks.

When the spores were germinated on beer-wort jelly and then transferred to sterilised bread, the first fruit bodies began to develop after sixty days and matured in eight days; from spore to spore the life cycle took sixty-eight days.

When the spores were sown directly on sterilised bread, the first fruit bodies appeared after forty-five days and matured six days later, thus giving fifty-one days from spore to spore.

When the mycelium was transferred from bread cultures to cubes of beechwood, the first fruit bodies matured 109 days after the spores had been germinated.

No fruit bodies were produced in cultures on beer-wort jelly.

In culture, the primordia developed in large clusters as small conical protuberances. In twenty-four hours the pileus was started. On the fourth or fifth day the primordia were well grown and began to stretch the veil. On the sixth to the eighth day the veil ruptured and the pileus expanded. The elongation of the stem is conspicuous from a very early stage (as in *Collybia apalosarca* var. *persitipitata*). There are no records on the exact time of rupture of the veil or on the period of maturity. The fruit bodies raised in culture were smaller than the wild ones, their pilei not exceeding 5 cm. wide and their stems being slender and more elongated.

The fruit bodies were grown mostly in the dark. If kept in continuous darkness the pilei were white; if grown in light, the pilei were dark brown at first becoming paler at maturity. If young primordia were transferred from darkness to light, they coloured up, but those transferred in later stages remained white. The fruit bodies matured equally well in darkness as in light.

In one culture there developed an irregular tremelloid fructification without a stem but with a normal fertile hymenium on the folds.

Development is angiocarpic. The primordial shaft has evidently the

same structure as that of *C. apalosarca*. But when the pileus is started, it is said that a layer of hyphae, parallel to the surface and two to three hyphae thick, covers the whole primordium: it is the universal veil, which becomes gelatinous at a later stage to form the slimy covering of the pileus and the infra-annular portion of the stem. When the pileus has formed, there is a layer of radiating hyphae distal to it which appears equivalent to the gelatinous hyphae in *C. apalosarca*. The gill cavity arises schizogenously between the limb and the stem and the marginal veil is formed from the "neutral" ground tissue left over in this part. When the pileus expands the universal veil has disorganised into the slimy covering and the marginal veil is pulled from the pileus to form the ring on the stem, which the author, wrongly surely, calls a superior annulus. The spores may ripen before the veil ruptures.

Fischer's interpretation of the development is scarcely borne out by his figures which show that his material was badly crumpled and distorted owing to fixation: the sections are oblique and the palisades therefore appear stratified with many layers of cells.

A close comparison between the rate of development of the fruit body in *Armillaria mucida* and that of *Collybia apalosarca* is scarcely possible as yet, since Fischer's material was raised in artificial culture, mostly in the dark, and the average temperature of the surroundings, which is not mentioned, could hardly have exceeded 20° C. unless an incubator was used. But a comparison with the fruit bodies of *C. apalosarca* var. *perstipitata*, which were raised on wood under natural conditions at an average temperature of 27° C., and which took four and a half to five days to reach maturity, suggests a doubling of the rate of development for a rise of 10° C., so that at the same temperature both should have the same rate.

Furthermore, Boursier(3) describes the presence of large cystidia, up to  $200 \times 40 \mu$ , on the sides and edges of the gills, the presence on the pileus of a compact palisade of clavate cells with more or less mucilaginous walls, and large oil drops in the basidia and the spores but not in the cystidia, which are simply vacuolate. Rea(22) also describes the cystidia on the gills as abundant, hyaline, fusiform or cylindric,  $90-140 (-180) \times 15-30 (-45) \mu$ .

#### THE COMPARISON BETWEEN *COLLYBIA RADICATA*, *C. APALOSARCA* AND *ARMILLARIA MUCIDA*

The size of the fruit body in all three varies roughly between the same limits: *Armillaria mucida* has on the average the smallest because the pileus does not exceed 10 cm. in width (according to published descriptions), and it may attain 15 cm. in the other two. So far

as possible at present, the points of agreement may be stated as follows:

(1) The pileus is dark fuscous brown or umber at first, becoming pale brown or greyish brown on expansion and finally pallid white, the colour being due to a pale umber pigment in the cell sap. In all three, very pale or colourless specimens may occur. It seems from the work of Fischer and Morquer that light is required for the development of the pigment.

(2) The mature pileus is plane or gibbous, not revolute or infundibuliform.

(3) The margin of the pileus is slightly incurved at first.

(4) The stem is stout, fibrous and homogeneous with the pileus.

(5) The gills are subdistant, broad, rather thick, waxy or submucilaginous, white, with a slight decurrent tooth and with a broad sterile edge: they become powdered with the spores.

(6) The flesh is white, rather soft, subhygrophanous, rather rapidly putrescent, fairly thick in the centre of the pileus but membranous in the distal part of the limb.

(7) The spores are white, large, subglobose or broadly ellipsoid, about  $16\mu$  wide, multiguttulate, and with a fairly thick wall, *ca.*  $0.5\mu$ . The basidia are correspondingly large, *ca.*  $65 \times 20\mu$ , and multiguttulate.

(8) The cystidia are large, smooth, thin-walled, vacuolate and abundant: the pleurocystidia are mostly ventricose, *ca.*  $150 \times 30\mu$ , the cheilocystidia mostly clavate and smaller, *ca.*  $80 \times 20\mu$ , though the cheilocystidia have not definitely been described in *A. mucida*.

(9) There is at least one compact palisade on the pileus, and there is probably a loose palisade of caulocystidia.

(10) The mechanism of the fruit body is Buller's *Armillaria* subtype.

(11) The mycelium is saprophytic on wood.

They differ in these respects:

(1) **The pileus.** A single palisade occurs in *Collybia radicata*, two in *C. apalosarca*. The gelatinous layer of *C. apalosarca* is absent from *C. radicata*. *Armillaria mucida* has probably both palisades with included jelly.

(2) **The stem.** The palisade in *Collybia radicata* differs from that on the supra-annular portion of the stem in *Collybia apalosarca* in the marked inflation of the subterminal cells and the presence of the umber pigment in many of them. Information about *Armillaria mucida* is lacking.

The surface of the infra-annular portion is viscid in *A. mucida* though the cause is uncertain: it is dry in the other two.

The motor tissue lies in both infra-annular and supra-annular portions in *A. mucida*; this state, which is usual in agarics, can be called the "perstipitate." In *Collybia apalosarca typica* the motor tissue is

confined in the supra-annular portion, and this state may be called *supra-stipitate*, cf. *Amanita* and *Volvaria*. *Collybia apalosarca* var. *persistipitata* agrees with *Armillaria mucida*. *Collybia radicata* is perhaps intermediate between the two extremes although it is impossible to say definitely before the primordia have been examined. This relation is shown in Fig. 11.

There is a disc in *C. apalosarca typica*, absent from the others, although there is a distinct swelling of the stem at a corresponding level in *C. radicata*, i.e. at ground-level where "root" and stem join.

(3) **The root.** It is best developed in *C. radicata*. It is reduced to a microscopic plug in *C. apalosarca typica* and var. *persistipitata*: this, too,

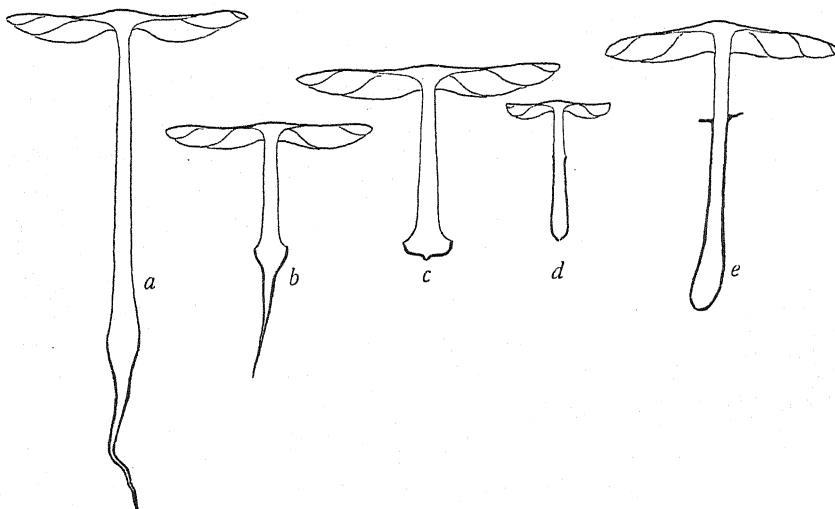


Fig. 11. Sagittal sections of mature fruit-bodies: *a*, of *Collybia radicata*; *b*, of *C. apalosarca* f. *radicans*; *c*, of *C. apalosarca* *typica*; *d*, of *C. apalosarca* var. *persistipitata*; *e*, of *Armillaria mucida*; the portions of the stem homologous with infra-annular portion in *A. mucida* shown by a heavy line.

must be the condition in *Armillaria mucida* and the rootless form of *Collybia radicata* described by Lange (16). In *C. apalosarca* f. *radicans* the root is often as well developed as in *C. radicata*. It is an opportunist growth made when the primordial shaft has a considerable distance to cover before the pileus can be developed, and it is not a primary distinguishing character. The emergency is nearly always present in some degree in the fruiting of *C. radicata*: in Lange's rootless form the fruit bodies developed on exposed roots and had a slight swelling at the base of the stem.

(4) **The gills.** In *C. radicata* they are widely sinuato-adnexed and often almost free. In *Armillaria mucida* they are rounded adnate or

subdecurrent. In *Collybia apalosarca* in Malaya they are as often rounded adnate as adnexed, sometimes widely sinuate and occasionally nearly free, but Petch makes a point that they are either adnate or sinuato-adnate in Ceylon.

(5) **The veil.** In *C. radicata* there is apparently no veil. In *C. apalosarca* it is rudimentary and leaves only a faint ridge or zone on the stem. In *Armillaria mucida* it is well developed and breaks away from the margin of the pileus to form an inferior annulus on the stem.

(6) **The spores.** *Collybia apalosarca* has the largest spores, those of *C. radicata* being the same size as those of *Armillaria mucida* or a trifle smaller. But in all three there is so much variation that I have tabulated the measurements given by different authors (Table V).

Table V. Sizes of Spores in  $\mu$ .

Authority	<i>C. radicata</i>	<i>A. mucida</i>	<i>C. apalosarca</i>
Bresadola ( <i>Ic. Myc.</i> )	12-18 $\times$ 9-12	—	—
Buller ( <i>Fungi of Manitoba</i> )	9-12 $\times$ 6-7 ( <i>C. radicata</i> var.)	—	—
Corner	11.5-19 $\times$ 11-15	—	16-23 $\times$ 16-22
Fischer	—	14-16 $\times$ 8-9	—
Killermann ( <i>Nat. Pfl. Fam.</i> )	12-16 $\times$ 10-12	14, globose	—
Lange ( <i>Ag. of Denm.</i> )	15 $\times$ 10	13-18 $\times$ 12-16	—
Lloyd ( <i>Myc. Notes</i> , III)	15-17, globose	—	—
Massee ( <i>Eur. Fung. Flor.</i> )	14-15 $\times$ 8-9	15-16 $\times$ 8-9	—
Murrill ( <i>N. Am. Flor.</i> )	15-17.5 $\times$ 10-12.5	—	—
Petch	—	—	16-24, globose
Rea ( <i>Brit. Bas.</i> )	14-15 $\times$ 8-9	15-17, globose	—
Ricken ( <i>Die Blätt.</i> )	12-16 $\times$ 10-12	15-18, subglob.	—

In *Collybia apalosarca*, fruit bodies in one collection generally have the spores of the same size, 16-19  $\mu$  or 19-21  $\mu$  or 21-23  $\mu$ , so that the variations may be hereditary.

In *C. radicata* and *Armillaria mucida* they are often ellipsoid rather than globose.

(7) **The cystidia.** As already mentioned, the pleurocystidia in the Malayan material of *Collybia radicata* are clavate rather than ventricose and the cheilocystidia are subventricose rather than clavate. *C. radicata* var. *gracilis* Lange has the cystidia (? pleurocystidia), small and narrowly ventricose, ca. 40  $\mu$  long  $\times$  2-3  $\mu$  wide at the apex, but the

details are not clear. Exact description of the cystidia in *Armillaria mucida* is also lacking.

(8) **The manner of growth.** The fruit bodies in *Collybia radicata* and *C. apalosarca* generally develop singly and may be solitary or in troops. In *Armillaria mucida* they are tufted, *i.e.* many primordia arise close together and, developing equally, become connate at the base. Occasionally in *Collybia apalosarca* small tufts are formed, but usually when the primordia are so crowded one takes the lead and the others abort. The smaller average size of the fruit bodies in *Armillaria mucida* may result from the tufted habit.

(9) **The habitat.** The fruit bodies of *Collybia apalosarca* and *Armillaria mucida* develop on dead trunks and branches above ground. Those of *Collybia radicata* develop from dead roots, which are generally buried, and they appear therefore terrestrial, but they are not humicolous: sometimes they grow from the top of stumps, but on following the "root" it is found to pass through the upper rotten wood and arise from the xylem of the tree roots, and they have never been recorded as growing from standing or fallen trunks.

(10) **Geographical distribution.** *C. radicata* is evidently cosmopolitan, occurring throughout the north temperate zone, Africa, Ceylon, Malaya, Java and Australia. *C. apalosarca* has been found hitherto only in Ceylon, Java and Malaya and is clearly tropical. *Armillaria mucida*, on the other hand, appears to be a temperate species occurring in North America and Europe.

Now, admitting the following general propositions about the evolution of agarics, the interrelations of the three species can be interpreted phylogenetically:

(1) A single palisade on the pileus is a less advanced character than two palisades with included jelly.

(2) As indirect development is derived from direct development (8), so the restriction of the motor tissue of the stem to the supra-annular portion and the modification of the infra-annular portion into a supporting disc are advances on the general condition in which the motor tissue is co-extensive with the stem and there is no disc; the supra-stipitate is derived from the perstipitate. (The supra-stipitate appears to lead to the "destipitate" condition of Gastromycetes, by total failure of the motor mechanism, cf. the Secotiaceae and the inarticulate Hymenogastraceae.)

(3) Decurrent gills precede adnate and adnate precede adnexed: free gills are the latest, as the hymenium is worked off the stem which becomes solely an elevator. Adnato-decurrent gills are intermediate between decurrent and adnate gills; sinuate gills are intermediate between adnate and adnexed or free gills.

(4) The gymnocarpic state is primitive, the angiocarpic advanced.

- (5) Large spores are derived from the average ellipsoid spore,  $6-8 \times 4-5 \mu$ .
- (6) The humicolous habit precedes the lignicolous.

Firstly, therefore, taking each point in order, *Collybia radicata* is the least advanced; the other two are probably at the same level. The two states are not so different as they appear. With respect to the centre of the pileus in *C. radicata*, the long colourless pileocystidia are probably homologous with the primary mucilage hyphae in *C. apalosarca*; the large colourless clavate pileocystidia are probably homologous with the secondary mucilage hyphae and the terminal pileocystidia in the external palisade in *C. apalosarca*, and the small pigmented pileocystidia will then be homologous with the elements of the internal palisade in *C. apalosarca*. The two states differ chiefly through the modification of the primary hyphae of the palisade into mucilage hyphae in *C. apalosarca*.

Secondly, *Armillaria mucida* and *Collybia apalosarca* var. *persistipitata* are the least advanced: *C. apalosarca* is the most advanced and *C. radicata* is perhaps intermediate. That is to say, *C. apalosarca* has the best developed primordium. In connection with the stem, it may be remarked also that, if the development of mucilage hyphae on the pileus is an advance, so must be the mucification of the surface of the infra-annular portion of the stem in *Armillaria mucida*; it is a speciality, therefore, of *A. mucida*.

Thirdly, *Armillaria mucida* is the least advanced, *Collybia radicata* the most advanced, and *C. apalosarca* intermediate; but the differences are not great.

Fourthly, *C. radicata* is the least advanced, *Armillaria mucida* the most advanced, and *Collybia apalosarca* is intermediate.

Fifthly, *C. apalosarca* is the most advanced, having the largest spores, and *C. radicata* is the least advanced, especially in its variety from Manitoba, and *Armillaria mucida* is intermediate. The large multiguttulate spore in the three species must be derived from the small ellipsoid spores,  $6-9 \times 4-7 \mu$ , with homogeneous oily contents, which is common in *Collybia* and the related genera *Tricholoma*, *Clitocybe* and *Hygrophorus*.

Sixthly, there is no obvious decision. The point is mentioned in order to notice that *Collybia radicata* is not humicolous but lignicolous and radicicolous, even though the fruit bodies are borne on the ground. It is most important to discover whether the immediate ancestor of this group was humicolous or lignicolous; if humicolous, cf. *C. platyphylla*, then *C. radicata* would present the first step toward the arboreal habitat of the other two; if lignicolous, then *C. radicata* must be specialised in being limited to roots.

On three out of five counts, therefore, in respect of the structure of

the pileus, the veil and the spores, *C. radicata* is the most primitive. On the other two counts, in respect of the differentiation of the primordium and the attachment of the gills, *Armillaria mucida* is the most primitive. In respect of the gills *Collybia radicata* is the most advanced; in respect of the veil, *Armillaria mucida* is the most advanced: and in both these respects *Collybia apalosarca* is intermediate. In respect of the primordium and the spores *C. apalosarca* is the most advanced.

Clearly, none of the three is on the direct line of descent; each is specialised. To relate them in the simplest way, it is necessary to postulate at least two ancestral species, which may be called the first and second hypotheticals. Their interrelations are shown in Fig. 12.

The first hypothetical would be gymnocarpic, perstipitate, caespitose, with adnate or decurrent gills, dry pileus and stem, a single palisade on the pileus, and broadly ellipsoid spores about  $10 \times 7 \mu$ . The second hypothetical would differ in being hemiangiocarpic, i.e. with incipient marginal veil as in *C. apalosarca*, with two palisades

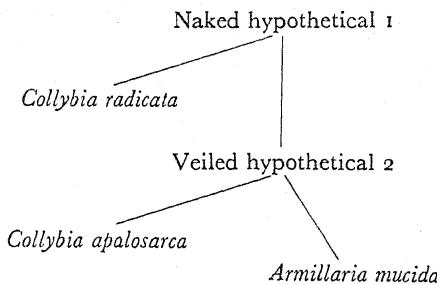


Fig. 12. The supposed genealogy of *Collybia radicata*, *C. apalosarca*, and *Armillaria mucida*.

with included jelly on the pileus and with the spores about  $15 \times 12 \mu$ . *C. radicata* differs from the first hypothetical in the radicicolous habit, the sinuato-adnexed gills and the larger spores. *C. apalosarca typica* differs from the second hypothetical in being supra-stipitate with a disc formed from the infra-annular portion of the stem, in the larger spores and in the subgregarious or solitary habit: the development of the disc is connected with the change in habit, because solitary specimens of the perstipitate variety without the disc are unstable: the fruit bodies of the two hypotheticals would derive their support from mutual pressure in the tuft, as in *Armillaria mucida*. *A. mucida* differs from the second hypothetical in being truly angiocarpic with an inferior annulus, and in the viscid surface to the infra-annular portion of the stem: a third hypothetical with a ring but a dry stem might therefore be postulated.

Whether the first hypothetical were humicolous or lignicolous with the arboreal habitat, *Collybia radicata* in becoming radicicolous would pass out of competition. If with the arboreal habitat, then both *C.*

*apalosarca* and *Armillaria mucida* would compete with it as well as the second hypothetical, and as both are derivative and obviously successful, they will have ousted the hypotheticals from the eastern tropics on the one hand and the north temperate zone on the other hand. But the second hypothetical may survive in the American tropics or in the south temperate zone, and it may be found among Spegazzini's species. And if, though it seems unlikely, the first hypothetical were humicolous, it too may survive somewhere.

#### RELATED SPECIES

It is not difficult, in spite of no detailed information, to find other species which are closely related to these three, for example *Clitocybe atrialba* (Murr.) Kauff., *Collybia Henriettae* W. G. Sm., *C. longipes* (Bull.) Berk. and *C. cheimonophylla* Berk. & Curt.

*C. atrialba* occurs in the southern states of North America (14). It is very close to *C. radicata* and differs chiefly in the decurrent gills and small spores (so it may prove the first hypothetical). It is radicicolous. The fruit body has essentially the same build as that of *C. radicata*, with a dark brown pileus, brown scaly markings on the stem, broad white subdistant gills and white flesh: the spores are subglobose or broadly ellipsoid,  $9-11\text{ }(-12) \times 7-9\text{ }\mu$ . The habitat suggests that other radicicolous species of *Collybia*, as *C. fusipes*, may be related either directly to the ancestral stock or from specialised offshoots, and perhaps even the humicolous (?) *C. platyphylla*, but these species may lack the palisades on the stem and the pileus. But if unrelated, whence have they come to this resemblance? *C. maculata*, which has a palisade of caulocystidia and which is also radicicolous and is placed in the same section of *Collybia* so that it cannot be separated generically at present, appears related to *Lentinus* (15), which is an utterly different stock of agarics!

*C. Henriettae* may be the same as the Malayan form of *C. radicata*. It is said to have a dry "somewhat downy" pileus (22); otherwise it is indistinguishable. Its rarity in England is understandable if it is the sporadic introduction of a tropical variety.

*C. longipes* is also close to *C. radicata*, again with the same habitat, the same build of fruit body and similar spores. But the pileus and the stem are dry, though they are evidently provided with palisades, a specific feature of which is the development of stiff brown hairs giving the macroscopic velvetiness. The spores are as variable: Ricken gives them as  $9-10 \times 6-7\text{ }\mu$  (24); Rea as globose,  $12-15\text{ }\mu$ , and  $10-11\text{ }\mu$  in var. *badia* Lucand (22); and Bresadola as globose,  $9-10\text{ }\mu$ , and  $13-15 \times 11-14\text{ }\mu$  in some Chinese specimens. The presence and nature of the cystidia are doubtful, since Ricken alone ventures "very sparse, subulate-cylindric,  $50-60 \times 8-10\text{ }\mu$ ," which recalls those of *C. radicata* var. *gracilis* Lange.

I have not had access to a description of *C. cheimonophylla*. But, as Boursier states that *C. alphetophylla* is only a variety of it (3) and as Patouillard's description of *C. alphetophylla*, quoted by Petch (19), is fully covered by that of *C. apalosarca*, *C. cheimonophylla* must be very close if not identical with *C. apalosarca*: on closer inspection, however, it may prove the second hypothetical.

Thus, in summary, there is a group of closely allied species in which the fruit body is gymnocarpic or angiocarpic and varies in size from very small (pileus 4 mm., stem  $3 \times 1$  mm.) to large (pileus 15 cm. stem  $20 \times 1.5$  cm.); in which the pileus is dry or viscid, with one palisade or two palisades and included jelly; in which the stem is perstipitate or discoid below and supra-stipitate, and dry or viscid; in which the gills are decurrent, adnate, sinuate, adnexed or nearly free; in which the spores vary between  $9 \times 6 \mu$  and  $23 \times 22 \mu$ ; in which the cystidia are sparse or very abundant, and vary in shape from sub-cylindric to clavate or ventricose and in size from  $50 \times 8 \mu$  to  $280 \times 40 \mu$ ; in which the habit is solitary or tufted, radiculous and terrestrial, (perhaps even humicolous), or lignicolous and high up on tree trunks, and extreme temperate or extreme tropical. The members of the group agree evidently in having fruit bodies of Buller's *Armillaria* sub-type, in having a palisade on the pileus and the stem, a fuscous umber pigment in the cell sap, at least of the pileocystidia, smooth white spores and thin-walled cystidia: probably it will be found that the spores and basidia are multiguttulate, and that the gill edge is sterile with a palisade of cheilocystidia. These properties are hardly distinctive.

#### THE GENUS *MUCIDULA*

It will be seen how unsatisfactory is the genus *Mucidula*. Some such unit is certainly required, but in our ignorance of the microscopic structure of toadstools how can it be defined? Thus I have preferred the Friesian form genera, though they are so artificial.

Patouillard made the genus to separate *Armillaria mucida* and *Collybia cheimonophylla* from *Armillaria* proper on the basis of the mucilaginous veil and the large spores. In view of the close relation between the species which have just been mentioned in the preceding section, these characters can no longer stand. Once the status of *Collybia apalosarca* is realised, *C. radicata* cannot be separated generically from *Armillaria mucida* in a natural system and *Collybia radicata* has no veil, a dry pileus in some cases and quite small spores in others. Nor can *C. longipes* or *C. atrialba* be separated generically, though still more unlike *Armillaria mucida*.

As emended by Boursier (3), the genus covers *A. mucida*, *Collybia cheimonophylla*, and *C. radicata* in a section "Viscidae" and *C. longipes* in a section "Pilosae." The generic characters are the large globose

spores, the large prominent basidia and cystidia, and the palisade of pileocystidia. The colour of the spores, the formation of the veil and the attachment of the gills are not mentioned, nor is an explanation given of "large" as applied to spores and cystidia, and it is not obvious from the range of sizes which I have just enumerated. *C. radicata* is placed in one section and *C. longipes* in another because the pileocystidia of *C. radicata* are mucilaginous. In this respect the Malayan form of *C. radicata* agrees with *C. longipes* and the sectional distinction fails: presumably, that is, for it is not explained. It is likely that *Armillaria mucida* and *Collybia apalosarca* differ more from *C. radicata* in the superficial structure of the pileus than *C. radicata* does from *C. longipes*.

But it is idle to multiply the genera. Before one can reclassify agarics on the sure lines of a natural system a thorough microscopic morphology must be instated; thorough research is first needed. To show how little is our knowledge of these organisms, one cannot point to a single exclusive property covering the members of this group, yet a natural genus is essentially exclusive, the species linking with other types of organism being extinct. One must search for the co-ordinate species with the brown colour, a sterile edge to the gill and the characters of the first hypothetical in *Collybia* and *Tricholoma*. Then may one look back in *Clitocybe* and *Hygrophorus* for the primitive members and forwards into *Pleurotus* for the most advanced, because it is natural to lignicolous Basidiomycetes with a mesopodal fruit body that they should evolve species with pleuropodal, apodal, sessile and resupinate forms. How do those with an upper gelatinous layer to the pileus and brown colouring, as *Pleurotus mastrucatus* Fr., *P. algidus* Fr., or *P. cyphellaeformis* Berk. or even *P. palmatus* (Bull.) Quél., compare? The field of research is unbounded.

#### THE MARGINAL VEIL

Concerning the nature of the veil there are two schools of thought. The older, which dates from de Bary (2), has been discredited. It was based chiefly on Brefeld's most detailed observations on *Coprinus* and Hartig's on *Armillaria mellea*. They said that the primordium of the fruit body was gymnocarpic, that the naked rudiment of the pileus was separated from the stem by a slight groove (formed by the annular outgrowth of the limb from the apex of the primordial shaft), and that hyphae grew out from the margin of the pileus and the surface of the stem and met and wove together to form the marginal veil across the groove, which, thus closed, became the gill cavity. To the contrary, the later school of Atkinson and the American mycologists (1, 11) has shown that in many species of *Psalliota*, *Hypholoma*, *Stropharia*, *Pholiota*, *Cortinarius*, *Inocybe*, *Tubaria*, *Lepiota* and in *Armillaria*

*laria mellea* itself the fruit body (comprising stem, pileus and gills) is laid down inside a primordium composed of "interwoven hyphae," and that the gill cavity arises as an annular split among the interwoven hyphae between the developing limb and the primordial stem and does not open to the exterior until the veil is ruptured on expansion of the fruit body. This original tissue of interwoven hyphae is called the ground tissue; that on the outside of the pileus and stem, covering the fruit body, is called the blematogen because it forms the universal veil, and that which persists between the margin of pileus and the stem forms the marginal veil, which is therefore not a later development subsequent to the pileus and stem.

My observations on *Collybia apalosarca* show that, so far from being antagonistic, the two schools of thought are complementary and each is based really on a partial view of the general developmental processes of the agaric fruit body. If it is borne in mind both that the pileus may be exogenous or endogenous and that the hyphae may grow from the margin of the pileus and the surface of the stem, reconciliation is easy. The two processes may be combined in different ways, and as there is abundant evidence for both, a brief description will explain. I have endeavoured also to present the idea visibly in Fig. 13.

Consider first the origin of the pileus. In the least specialised gymnocarpic agarics, such as *Craterellus* and *Cantharellus*, the pileus is exogenous. That is to say, the limb is formed essentially in the same way as I have described in *Polystictus xanthopus* (8), merely by displacement of the main growing region of the primordial shaft from the centre of the apex to the periphery; the peripheral hyphae at the apex of the shaft become the main hyphae of the marginal growing region of the pileus; but owing to epinasty, which is very marked in all agarics, the margin of the pileus tends to grow round towards the stem. But in the first step towards the angiocarpic type, it is not the ends of the main hyphae of the primordial shaft which form the limb but laterals from them: the limb thus arises a short distance below the apex of the shaft. Therefore here and probably in *Clitocybe*, *Hygrophorus* or *Collybia* including *C. radicata*, the pileus may be said to be slightly endogenous, though development in the main is still gymnocarpic (the gill cavity being open from the first), and there is no veil unless one can regard the free ends of the main hyphae of the primordial shaft over the centre of the pileus as the rudiment of the blematogen: such, too, may be the nature of the umbo in *Androsaceus*. In the next step, the hemiangiocarpic, occurring in *Laccaria laccata* (11) and *Collybia apalosarca*, the laterals forming the limb arise still more internally so that the layer of free hyphal ends over the primordial pileus is more conspicuous and is continuous with the palisade on the primordial shaft. There is, in fact, in this case a rudimentary blematogen,

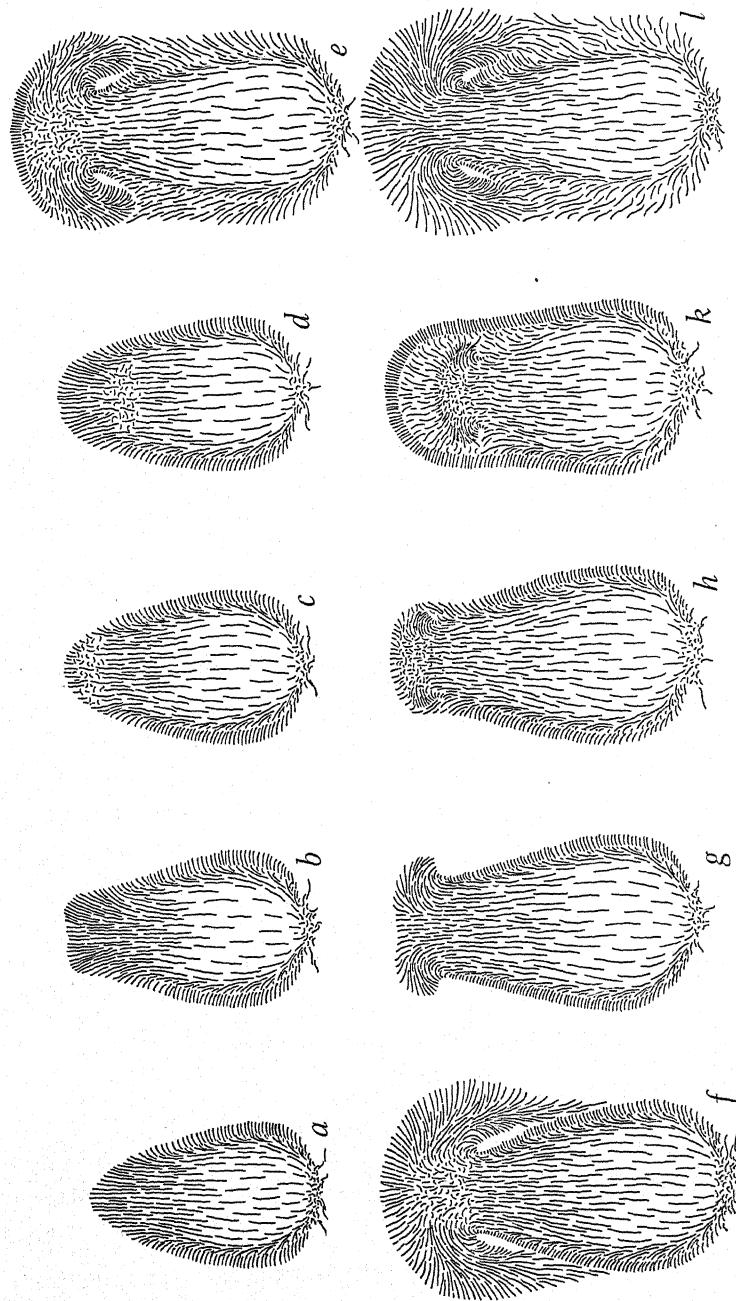


Fig. 13. A scheme showing the different methods of making the veins in agarics: *a*, the primordial shaft, corticated and with the medullary hyphae beginning to enlarge; *b* and *g*, developing a pileus exogenously; *c* and *h*, developing a pileus slightly endogenously; *e*, a gymnocarpic primordium with outgrowth from the surface of the stem; *f*, a gymnocarpic primordium with outgrowth from the surface of the stem and the margin of the pileus; *i*, a gymnocarpic primordium with outgrowth from the margin of the pileus.

because the palisade over the primordial stem and pileus grows for some while after the limb is started and it forms a thin universal veil which prevents the primordial limb from breaking through to the exterior: the gill cavity arises internally as a gap between the limb and the stem. Then lastly in the angiocarpic type, the laterals which form the limb arise very deeply at such a distance below the apex of the primordial shaft that a very thick layer remains distal to the pileus and forms the easily recognisable blematogen: the pileus is deeply endogenous and the gill cavity is closed from the first.

Consider then the second process. Hyphae may grow out from the surface of the stem and the margin of the pileus whether the pileus is exogenous or endogenous in any degree. Among gymnocarpic species there is a slight outgrowth from the margin of the pileus in *Clitocybe cerussata* which is more marked in *Clitopilus noveboracensis* (11), and it is most striking in the section of *Lactarius* including *L. torminosus*. Outgrowths from the stem are exceedingly common, for example the palisade in *Collybia radicata* or the shaggy villousness of *Paxillus atrotomentosus*. In *Pluteus admirabilis* one has an example of outgrowth from the pileus in a species in which the limb is probably slightly endogenous: hyphae grow from the incurved margin of the primordial limb and interweave loosely with hyphae on the stem but insufficiently to form a marginal veil (11). This case leads to the similar condition in the hemiangiocarpic type shown by *Collybia apalosarca*: the very rudimentary blematogen is reinforced by outgrowths from the pileus and the stem, but again insufficiently to form a ring. This in turn leads to the angiocarpic species. In *Tubaria furfuracea* and *Armillaria mucida* the pileus is fairly deeply endogenous and in *Psalliota* it is very deeply endogenous, yet such marginal outgrowth from the pileus occurs abundantly in these species (11): in *Pholiota squarrosa* and *P. flammans* it is particularly extensive (11). Then in *Coprinus ephemerus*, *C. ephemeroides*, *C. lagopus*, and *C. stercorearius*, according to Brefeld, one has the rare combination of an exogenous pileus with subsequent angiocarpic development through such secondary outgrowths which are mainly from the base of the stem. And I see no reason to doubt, as Atkinson does, his observations on the ground of poor technique; for, it may be remarked in this connection, that a great deal more can be learnt about the development of fruit bodies from hand sections of fresh material than from microtome sections: the sections must be thick in order to trace the course and branching of the hyphae, and while fairly thick sections of fresh material are still beautifully transparent, thick microtome sections are opaque and in thin ones the hyphae are chipped into bits and cannot be followed through the tissue.

The presence of a universal veil depends primarily on whether the pileus is exogenous or endogenous: the presence of a marginal veil

depends more particularly on the outgrowths from the margin of the pileus and the stem. If the amount of both blematogen and marginal growth is small, there will be a cortina of varying thickness, e.g. *Tricholoma* and *Cortinarius*; if the blematogen is practically absent and marginal growth slight, the veil will be as rudimentary as in *Pluteus admirabilis* or *Collybia apalosarca*. If the amount of both is great, then the universal veil forms scales on the pileus and the infra-annular portion of the stem and the marginal veil forms the inferior annulus, e.g. *Armillaria* and *Pholiota*; if the marginal veil separates from the stem as well as from the pileus it forms the movable ring, e.g. the supra-stipitate species of *Lepiota* as *L. procera*. If the amount of blematogen is small and the marginal outgrowth of the pileus relatively great, the marginal veil is torn from the stem and is appendiculate from the edge of the pileus, e.g. *Hypholoma appendiculatum* (and perhaps *Panaeolus sphinctrinus* etc.). If the blematogen is very well developed, coherent and separated from the pileus by a cleavage layer of loose aerenchymatous or gelatinous tissue, the universal veil forms the volva as the pileus slips out of it, e.g. *Amanitopsis* and *Volvaria*.

There is the final complication in the *partial veil*. It is formed from hyphae which have grown from the surface of the stem into the gill cavity, and it is really only an elaboration of the palisade on the supra-annular portion of the stem as the proximal part of the universal veil is an elaboration of that on the infra-annular portion. In its most highly developed state in *Amanita* and *Psalliota*, the palisade forms a thick coherent tissue firmly connected with that of the marginal veil, which is also well developed. On expansion of the primordium both the marginal veil and the partial veil are peeled off the stem from below upwards and stretched as a membrane under the gills, but when the pileus is half-expanded the partial veil is torn from the marginal veil and drops back on to the stem as a loose sheath pendant from the apex and known as the superior annulus: the marginal veil is thus appendiculate in fragments from the pileus. Nevertheless one can perceive in *Collybia apalosarca* the rudimentary homologue of the partial veil in the palisade on the supra-annular portion of the stem, as well as the homologue of the blematogen in the loose cortex of the primordial shaft, and the homologue of the marginal veil in the anastomosis between the margins of the limb and disc. In *Amanita* these slight outgrowths have become thick, recognisable layers and ornaments to the umbrella.

The difficulties met with in comparing the development of the fruit body in agarics are mainly difficulties of description. One cannot delimit exactly the parts; the stem merges into the pileus and the pileus into the gills; the surface of the pileus merges into the universal veil and this into the marginal veil which merges into the partial veil; even the hymenium may be ill-defined as it often occurs

on the stem for some distance below the gills. But in studying the development one must determine the sequence of the hyphae in their manner of apical growth and branching in the primordium, before the interrelations of the parts can be understood. In mature fruit bodies, whether gymnocarpic or angiocarpic, the hyphae in the stem, limb and gills are nearly always longitudinal with respect to the parts (though a curious exception may occur in *Gyroporus castaneus* in which the main hyphae in the stem appear transverse or tangential!), and the hyphae of the stem are joined as laterals to those of the mycelium, the hyphae of the limb as laterals to those of the stem apex, and the hyphae of the gill trama as laterals to those of the limb. The sequence implies acropetal development of the whole fruit body with apical growth of the parts and subterminal branching originating each part successively: the base of the stem must be formed first, then the shank of the stem, then the limb, and lastly the gills. One cannot imagine how else the parts may develop when there is this connection between their hyphae, yet several investigators affirm that it is by no means always so. It is said that the hymenophore is "differentiated" first in *Armillaria*, *Psalliota* and *Stropharia*, and that the pileus is "differentiated" first in *Hypholoma*, *Tubaria*, *Amanitopsis* and *Amanita*, so the parts must then float into existence independently in the primordium and subsequently become joined together, rather in the way that the Cheshire cat came upon Alice in Wonderland. But, of course, all primordia are initiated as a primordial shaft, the body of which becomes the stem, and the stem is therefore always the first part to be defined. Nor is it clear how the inception of the parts is recognised, as it is stated, from their "differentiation": there is no differentiation of the hyphae according to the parts, the fruit bodies being monomitic, and the differences in staining power of the hyphae, which are shown in the explanatory microphotographs, are caused by the vacuolation of the cells and alterations of the hyphal walls, and such processes succeed inception of the parts. I am inclined to turn the tables and champion Brefeldian technique against Atkinson's: though there are many papers on the subject<sup>(13)</sup>, I doubt if anyone could describe even how the common mushroom is formed inside a body of interwoven hyphae by the apical growth and branching of another set of hyphae. But when development is explained as the consequence of the properties of hyphae in an organic whole, such notions may also fade into a smile.

#### MORPHOLOGICAL REMARKS

*Collybia apalosarca* shows well a common factor in the equipment of multifilamentous plants, whether algal or fungal. It is the formation of a level at the surface or boundary of a tissue by sympodial branching. The factor becomes particularly important in agarics through the

development of the palisades and their elaboration into the veils. In both alga and fungus the level results from the manner of growth of the soma. Apical growth is retarded in the filaments at the periphery of the growing point and their free ends are splayed aside by the laterals which continually arise in the centre of the growing point. As they accumulate, therefore, the free ends of the peripheral filaments are perforce rotated through more or less of a right angle and come to point outwards perpendicularly to the long axis of the soma. A longitudinal section of such a growing point reveals the fountain effect of Oltmanns—his “springbrunnen-typus” (18). But here comes the difference. In both algae and fungi the medullary filaments, composed of the fixed proximal parts of the filaments, begin to enlarge and without some compensatory process the free cortical filaments would be pulled apart to form a sparse pile of hairs. In algae the free ends of the filaments continue to grow out, branching repeatedly, and they form the compact, small-celled, photosynthetic cortex, the increase in surface of which may exceed that allowed by the enlargement of the medulla and so the medullary filaments may be pulled apart to form mucilage spaces or air cavities. In fungi, on the contrary, the outgrowth of the free ends is soon arrested: laterals then arise from the subterminal cells and, on reaching the level of the terminal cells of the parent filaments, they stop growing and branch sympodially in their turn: a palisade of greater or less density is thus constructed. In fungi, moreover, the cells of the palisade, not being photosynthetic or absorptive, generally enlarge also. In the simplest cases, as in *C. apalosarca*, only the terminal cells enlarge but in many others, in the palisade on the stem of *C. radicata* or in the cortex of the apothecium in Discomycetes, for example, one or more of the subterminal cells enlarge and a compact pseudoparenchymatous layer is constructed. In few fungi, however, is the intercalary growth of the sterile palisades sufficient to prevent disruption on expansion of the primordium: in most, the palisades are broken up into squamules or scurfy or pruinose particles. But the hymenium is never disrupted because such enormous numbers of basidia are intercalated: it often happens, instead, that the hymenium disrupts the medulla, as in *Physalacria*, *Pistillina* and many other Clavariae and the Clavuleae.

The branching and inflation of the cells of the palisades in fungi also enables one to recognise a characteristic plectenchymatous underlying layer or *hypoderm* of which the subhymenium is merely a special case. The hypoderm comprises the proximal parts of the hyphae of the palisade and they are always closely interwoven or interlocked because the laterals in finding their way to the surface push between the pre-existing hyphae and often arrive at some distance from their parent hyphae. Then, on inflation, their cells are pulled this way and that and often become looped and stretched and still more entangled

with each other. Thus the hypoderm, including the subhymenium, always develops after the palisade, including the hymenium, has been defined.

The time-factor must enter into comparisons not only of the size and degree of development of parts but even of the shape of the individual cells. Dimorphism between cheilocystidia and pleurocystidia occurs in many genera which are not nearly related, as in *Inocybe*, *Pluteus*, *Psathyra* and *Mycena*, and it may generally be a matter of unequal development through the late inception of the cheilocystidia, just as in *C. apalosarca*. The large ventricoso-fusoid pleurocystidia, and pileocystidia, must pass through a clavate stage during the inflation of the cylindric terminal cell and their final shape is reached through the protrusion of the apical part. If growth is arrested before development is completed, the cystidium will have an unfinished appearance. Thus, in cases of dimorphism, the cheilocystidia are mostly clavate and of simpler structure than the pleurocystidia and there are transitions on either side of the gill edge, e.g. *Inocybe*, or *Pluteus*, with thick-walled ventricoso-fusoid pleurocystidia and thin-walled clavate cheilocystidia. As the pileocystidia of *C. apalosarca* pass through a clavate stage, so may one expect the less advanced species in the group to have clavate pileocystidia, e.g. *C. radicata*. The caulocystidia of *C. apalosarca* are also clavate because they are among the last terminal cells to be inflated. It will be interesting to learn the nature of the hairs of *C. longipes*; for this species is gymnocarpic and the normal acropetal development of the palisades should be less transposed and large caulocystidia would be expected.

The non-inflation of the cells of the hyphae forming the internal palisade of the pileus in *C. apalosarca* illustrates another common feature in the histology of fungi. In a gelatinous tissue, in which the walls of the hyphae are mucified, the constituent cells are rarely inflated. It seems that the mucilage absorbs the water which is normally available for the inflation of the cells, or that some alteration of the plasma membrane, following mucification of the wall, prevents the cells from developing their normal osmotic system.

#### SUMMARY

The structure and development of the fruit body of *Collybia apalosarca* B. & Br. is described in detail as a multifilamentous soma formed by the apical growth and ramification of hyphae with modification of the cells on cessation of growth.

A specific description is given, based on Malayan material, and a new variety *persipitata* and a new form *radicans* are proposed.

In the mature fruit body all external and internal surfaces between tissues are bounded by palisades of free hyphal ends the terminal cells

of which have characteristic shapes. On the pileus there is a thick gelatinous layer derived from the blematogen and bounded by an external and an internal palisade.

Development is indirect and hemiangiocarpic. A short, loosely corticated primordial shaft is first formed. At the apex of the shaft the limb arises slightly endogenously. There is a rudimentary blematogen with a rudimentary marginal veil reinforced by the outgrowth and anastomosis of hyphae from the margin of the pileus and the surface of the stem, but there is no ring or cortina. The gill cavity is more or less closed at first. Development is strictly acropetal with apical growth of the parts of the fruit body followed by intercalary growth at the surfaces by sympodial branching, which multiplies the tissue-elements and compacts the palisades, and finally with inflation of the medullary hyphae causing expansion of the primordium. The base of the primordial shaft becomes the base of the stem; the body of the shaft becomes the shank of the stem; the apex becomes the centre of the pileus while the limb is formed by marginal growth from the apex of the shaft and the gills by marginal growth in centrifugal lines on the proximal side of the limb. Inflation of the hyphae proceeds acropetally from the base of the stem and reaches a maximum in the supra-annular portion of the stem and the central portion of the limb on the night of expansion. In the typical form the infra-annular portion of the stem is enlarged into a supporting disc which does not elongate; in var. *persitipitata* the stem elongates throughout and there is no disc.

Biologically, the fruit bodies belong to Buller's *Armillaria* subtype.

By correlating in different fruit bodies the average elongation of the cells in the mature stem with the length of the mature stem, it is shown that the great variations in size of the fruit body (from 3 mm. to 9 cm. high) are due either to juvenescence or to differences in the inflation of the cells.

The arrangement and number of the gills are also correlated with the size of the fruit body. Those with a thick stem apex generally have more primaries than those with a thin stem apex, and those with a wide limb more ranks than those with a narrow limb, from which conclusion additional proof is given that small fruit bodies are generally juvenescent.

*C. apalosarca* is intermediate in many respects between *C. radicata* and *Armillaria mucida*. The three species are compared as fully as possible. The structure of the mature fruit body of *Collybia radicata*, as it occurs in Malaya, is described and the relevant facts about *Armillaria mucida* are summarised.

In all three species the construction of the fruit body is essentially the same. But *Collybia radicata* has a single palisade on the pileus,

without a gelatinous layer, and is evidently gymnocarpic. *Armillaria mucida* has evidently the same structure of the pileus as *Collybia apalosarca* but is angiocarpic with an inferior annulus. These and other minor differences are evaluated by certain general propositions concerning the evolution of agarics. The three species are considered specialised offshoots of two hypothetical ancestral species: while the first hypothetical is probably extinct, the second may be found in tropical America or the south temperate zone.

The morphology of the marginal veil is reconsidered. The investigation of *C. apalosarca* shows that there is really no antagonism between de Bary's early account and that of the modern American school, since each is based on a common developmental process in agarics and is partly correct. The formation of the marginal veil may depend on the outgrowth and anastomosis of hyphae from the margin of the pileus and the surface of the stem, as de Bary held, as well as on the presence of a blematogen, as the American school maintains: both factors may be equally important, or the one or the other ascendant. It is shown further how the presence of the blematogen depends on the endogenous origin of the limb and how the marginal veil is related to the universal and partial veils.

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## PHYTOPHTHORA MEGASPERMA DRESCHLER IN TASMANIA

By W. J. DOWSON, M.A., D.Sc.

*Lecturer in Mycology, Cambridge University; late Plant Pathologist,  
Department of Agriculture, Tasmania*

IN the Tasmanian autumn, *i.e.* April–May, of 1931, many complaints were received by the Department of Agriculture of Tasmania from Sydney, New South Wales, relating to the bad condition of carrots exported from the north-west coast of the island State.

Carrots have been grown for export for some years in the reclaimed swamps round the town of Smithton where heavy yields are obtained. The crop is dug, bagged immediately and sent by lorry or train to the port of Stanley to await shipment to the mainland, either direct to Sydney or by a longer route along the north-west coast of Tasmania and thence to Sydney. The sea journey occupies from two to four days according to the route taken, and the carrots remain enclosed in the bags for about a week.

The autumn of 1931 was abnormally wet so that the crop was dug, bagged and transported to Sydney under exceptionally humid conditions. A sample of a consignment returned from New South Wales was in such a rotten condition as to render diagnosis of the possible cause impossible; but the most striking symptom was a black discolouration of the tissues. The Port Inspector at Stanley was warned to look out for dark soft marks, during his inspection of carrots for export. This resulted in a sample being sent to the laboratory at Launceston with the information that the contents were probably what the Sydney inspectors were complaining of. At about the same time a further sample was returned to Tasmania from Sydney in not quite such a bad state; on comparing the two samples the rotting seemed to be similar.

The lowermost part of the roots, often including the very apices, was soft and black. Various fungi including *Rhizoctonia* (*Corticium*) *Solani* were observed in the surface layers of the cortex of such diseased areas, but the blackening did not extend beyond these and the rotted interior was never discoloured, only "water-soaked" in appearance.

Microscopical examination of the softened tissue, particularly at the edge next to sound areas, revealed a fairly abundant intercellular mycelium composed of relatively stout aseptate hyphae. Further examination showed that in the blackened layers of the cortex exceedingly numerous spherical, thick-walled resting spores were present, recalling in appearance the oospores of a Phycomycete.

No difficulty was encountered in isolating the aseptate mycelium which grew slowly on potato agar with a rather diffuse growth. Better growth resulted in hanging drop cultures of potato agar, possibly because these were more humid than plate cultures. Luxuriant growth took place on steamed plugs of carrot and potato. Oogonia and antheridia, mostly of the amphigynous type, were produced on the above media but all attempts to induce the formation of sporangia were unsuccessful.

Further subcultures were made in England on other media such as potato-glucose agar, oat-meal agar and corn-meal agar; on all there was a luxuriant growth with the production of sexual organs but no sporangia. When pieces of mycelium from plates of any of the above media were placed on slices of young, fresh carrots, kept moist in deep Petri dishes at a temperature of 25° C., a slow rot developed in the course of some weeks similar in appearance to that observed in the original carrots. No infection was observed through the unwounded surface and none was obtained when portions of mature carrots were inoculated.

At this point cultures were sent to the Imperial Mycological Institute where the *Phytophthora* was identified as *P. megasperma* Dreschler (*Rev. Appl. Mycol.* II, 302) and, following the advice of Mr S. F. Ashby, sporangia were eventually obtained in water cultures a fortnight old.

Information from Tasmania showed that no complaints had been received from New South Wales during the season 1931-2 which was very much drier than the previous season: it would seem that the abnormally wet conditions were primarily responsible for altering the general equilibrium between carrots and soil-dwelling fungi in favour of the latter. Under such conditions infection probably took place, and there is no doubt that once infected the invasion of the tissues developed rapidly during transit, more particularly in the steamers' holds.

## NAUMOVIA ABUNDANS DOBROZR.

By J. RAMSBOTTOM

(With Plate I)

IN 1926 the late Mr D. A. Boyd sent me a specimen of a Pyrenomycte growing on *Prunella vulgaris* which had been gathered by Miss M. L. Miles at Caputh, Perthshire in Sept. 1912. I was unable to find spores and could make no guess at its identity: this I believe was also the experience of other mycologists to whom specimens were sent. The following year, after the Aviemore foray, I found the fungus on a wayside bank just above Pitlochry. Again I was unable to find spores.

Shortly afterwards a description of the fungus by Dobrozrakova appeared in *Morbi Plantarum*, xvi (1927), 197-9, with the name *Naumovia abundans*. It had been first observed by N. A. Naumov in the Luga district of Russia but in an immature state. Dobrozrakova gathered it from a rather wide area in July, 1926, and, in order to obtain ripe asci, she marked some plots containing infected plants and transplanted others; the fungus was found fully mature in both series the following May and June.

*Naumovia* was gathered in abundance at the Belfast Foray (1930) and I found it later at Monaghan though it had not been noticed in three weeks' general collecting farther south. It has also been gathered in several districts in England, e.g. Newcastle, Leicester, Haslemere.

I made two attempts to transplant infected plants to my garden but, probably on account of delay, without success. I therefore asked my colleague Mr George Taylor to look for old infected stems when botanizing in Scotland and he succeeded in obtaining mature fruits at Reston, Berwick, in April, 1933 (Pl. I, figs. 3 and 4).

Infection may occur when the host plant has only two or three leaves. All vegetative parts of the plant are affected except the roots and the flowers though the stalk of the inflorescence is often crowded with perithecia. The general appearance of the fruit bodies is shown in Pl. I, fig. 1. According to Dobrozrakova "strongly infected plants look depressed, do not flower, or the inflorescence is shortened and the flowers fall off prematurely." On the whole one may say that the fungus develops most markedly in moist places though it is to be found in dry habitats. The original diagnoses are as follows:

**Naumovia.** Stromatibus firmis, carnosō-lignosis, bene evolutis et delimitatis, longitudinaliter confluentibus, subepidermicis, dein liberis, atrofuscis, parenchymaticis. Peritheciis superficialibus, papil-

lato ostiolatis. Ascis cylindraceis, a paraphysatis; sporidiis filiformibus septatis subhyalinis.

*N. abundans*. Peritheciis stroma insidentibus, 10-20 et multis longitudiner, aggregatis, sphaericis, 225-350  $\mu$  diam., epidermide primo tectis, dein rima longitudinali prorumpentibus et definitive liberis. Stroma ac parietibus peritheci parencymaticis. Ascis cylindraceis, breve pedicellatis, chlorinis, 67-97  $\mu$  long., 4.5-7.5  $\mu$  cr., basi coalitis. Sporidiis biseriatis, filiformibus, utrinque acutiusculis, rectis v. sepius curvulis, multiguttulatis, dein multiseptatis (1-6), 30-39.5  $\mu$  long., 1.5-3  $\mu$  cr., subhyalinis.

Hab. in planta tota: caulis, stolonis, foliis et inflorescentiis vivis *Brunellae vulgaris* parasitice.

Dobrozkova places it in Cucurbitariaceae near to *Gibberidea*.

The British specimens agree perfectly with this description, measurements of the Reston specimens being, perithecia 250-350  $\mu$  diam., ascii 60-100  $\times$  4-7  $\mu$ , spores, slightly curved, 38  $\times$  2  $\mu$  (average).

The records of *Naumovia* in Great Britain suggest that it first became common in Scotland and that it spread thence to the southern counties of England.

Dobrozkova says "it is difficult to understand why this parasite has not been noticed before, since its effects are very characteristic." In my experience heavily infected plants tend to have an etiolated appearance often being elongated and somewhat yellowish.

It would be remarkable if Miss Miles and N. A. Naumov should stumble across such a well-marked and characteristic fungus as they did if it had always been as common as it is now. When I found it at Pitlochry I was hurrying along in a very heavy thunderstorm and merely stopped to gather some plants which were obviously diseased; I saw that a fungus was present but I could not then see what it was. It is only comparatively recently that mycologists generally have begun to look for the fungus: previously it was the diseased *Prunella* that was gathered and the fungus thus found. Those who first saw *Naumovia* at the Belfast foray will recollect that this was their experience.

This being so it is inconceivable that the fungus should have been overlooked until recently and then be constantly found independently by different mycologists who were unaware of its identity.

Is the fungus a recent introduction to this country? It is always unsafe to suggest such a hypothesis when the host plant is uncultivated. If it is a recent introduction whence did it arrive? A sudden appearance of a fungus is always a matter of interest from the standpoint of distribution and there are many records of such phenomena in our own literature. The present example differs from these, however, in that the fungus is not one known previously elsewhere, and being introduced to new conditions becomes epidemic usually to become

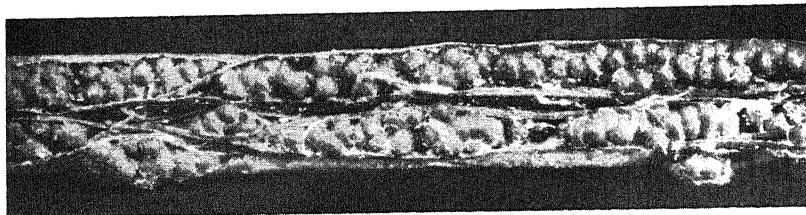


Fig. 1

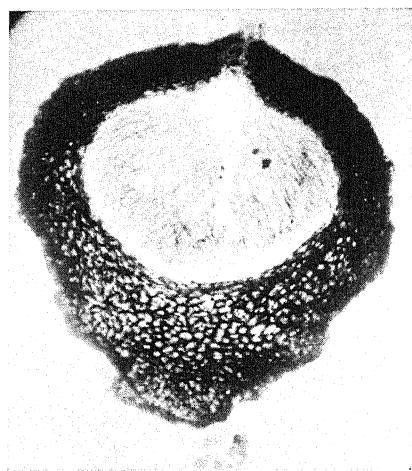


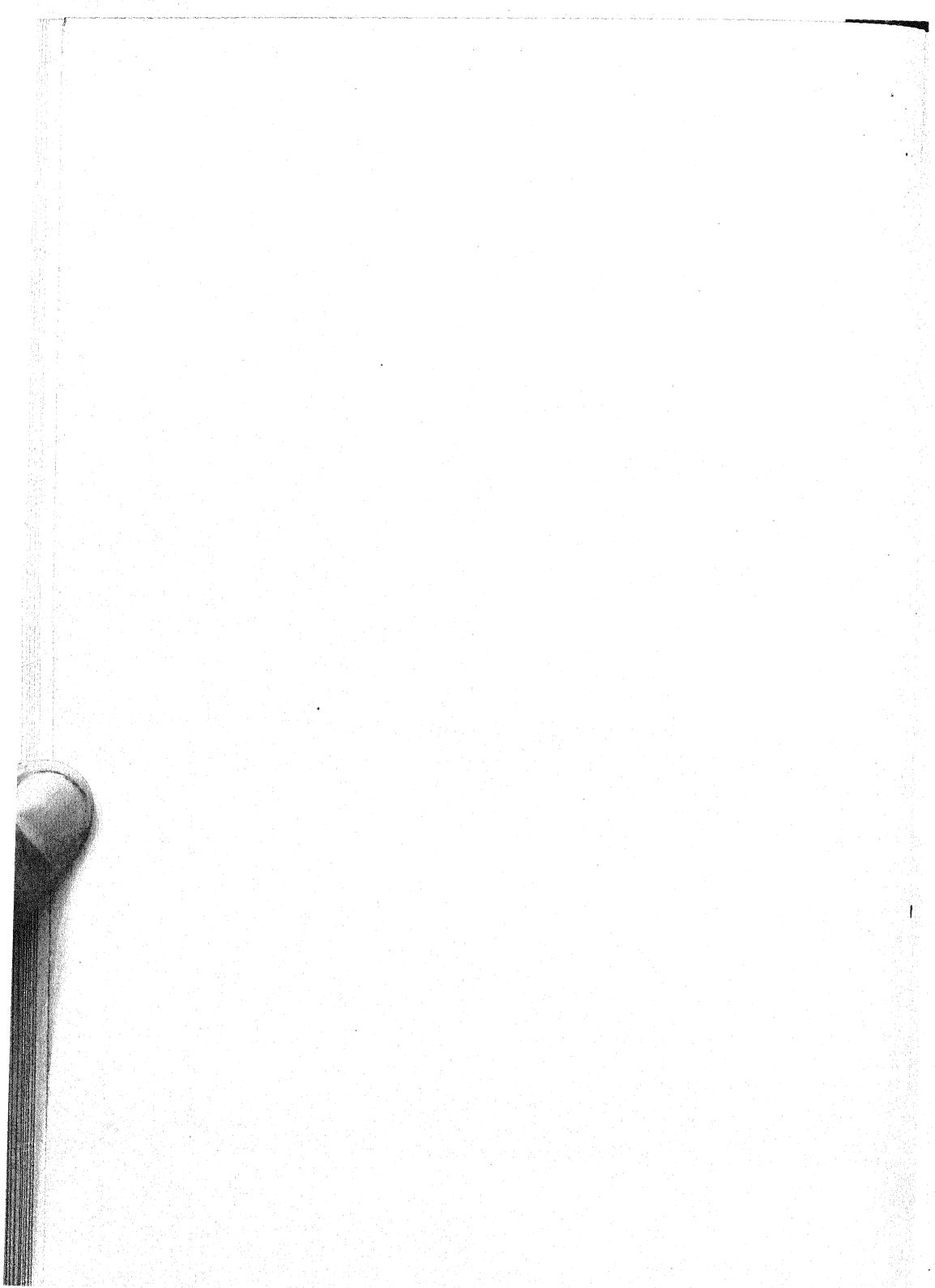
Fig. 3



Fig. 2



Fig. 4



much less rampant later. So far as I have been able to find out *Naumovia* has not been lurking under another name—it is an entirely newly described fungus.

We speak loosely of “new species” and “new genera” sometimes as if they were really new creations and not merely descriptions or diagnoses. Here there might be a temptation to consider the fungus as an entirely new entity and to offer suggestions about how it might have originated. It would certainly be an interesting phylogenetic exercise to tax one’s ingenuity in suggesting the possible evolution of so characteristic a Pyrenomycete but it would entail nothing but sterile speculation. All that we can say with certainty is that *Naumovia abundans* was first noticed in Scotland in 1912 and in Russia in 1926 and that it is now widespread in the British Isles, often occurring in considerable quantity.

I wish to thank Miss F. L. Stephens for help in section-cutting, Mr E. H. Ellis for the photomicrographs and Dr B. P. Uvarov for translating Dobrozrakova’s paper.

#### EXPLANATION OF PLATE I

Fig. 1. Infected stem of *Prunella*. The infection was heavy from the tip of the inflorescence to the rootstock ( $\times 11$ ).

Fig. 2. Section of peritheciun and host ( $\times 20$ ).

Fig. 3. Section of mature peritheciun ( $\times 144$ ).

Fig. 4. Ascii and spores ( $\times 1100$ ).

## PROCEEDINGS

Meeting held at University College, London, Jan. 20th, 1934,

Dr B. Barnes, President, in the Chair.

### A. H. REGINALD BULLER. *Omphalia flava*, a Luminous and Gemmiferous Leaf-spot Fungus.

*Omphalia flava*, the cause of the American coffee-leaf disease, is a luminous and gemmiferous leaf-spot fungus. It attacks not only coffee leaves, but also the leaves of a great many different hosts included in the Dicotyledons, Monocotyledons, and Ferns.

In pure cultures, as Ashby first observed, the mycelium produces in succession: (1) *gemmae*, hitherto misnamed "Stibium-bodies," and (2) perfect agaricaceous *sporophores*.

Each gemmifer is yellow and consists of a slender solid tapering *pedicel* about 2 mm. long and of a terminal, detachable, multicellular *gemma*, shaped like the knob of a door-handle and about 0.36 mm. in diameter. The structure of a gemmifer has been redescribed in detail. The *gemma* is regarded as a reduced, gillless, sporeless, detachable pileus. A *gemma*, after being blown by the wind on to a leaf, sends out hyphae which penetrate the epidermis and produce a leaf-spot. On the leaf-spot about thirty to fifty new gemmifers are soon developed. The leaf-spots on coffee leaves owe their origin to *gemmae* which seem to have largely taken the place of basidiospores as a means of propagating the species.

The mycelium and *gemmae* of *Omphalia flava*, both in artificial cultures and in leaf-spots, are luminous. This discovery has provided a means for diagnosing the American coffee-leaf disease in the dark. At night, in a Porto Rican coffee plantation, Professor Albert Müller was able to see coffee leaf-spots very clearly at a distance of 2-3 ft. from the leaves and less clearly, although distinctly, at a distance of 6-10 ft.

### KATHLEEN SAMPSON. The Presence and Absence of an Endophytic Fungus in *Lolium temulentum* and *L. perenne*.

A critical survey of the literature indicates that it is incorrect to assume, as certain writers do, the identity of the seed fungus of *Lolium* and the organism, apparently a Phycomycete, which occurs in the roots.

The following observations refer to the first fungus, an intercellular endophyte of uncertain affinity which invades the vegetative organs and the seed.

Single plants of *L. temulentum* selected in 1929 formed the starting-point for pure lines which have been studied during four seasons. The presence or absence of the fungus was determined by an examination of pith scraped from a flowering stem and stained with cotton blue. Ovaries and seeds which were sectioned confirmed the results obtained by this method.

Lines classified on this basis remained true to type for four generations. When reciprocal crosses were made, the hybrid was infected only if the female parent carried the fungus. This made it possible to compare plants of similar genetical constitution which differed only in the presence and absence of the fungus. Two series of *F*<sub>1</sub> plants produced by reciprocal crossing and examined in regard to growth, yield and chemical composition, gave no indication of either a stimulating or a depressing effect resulting from invasion by the endophyte.

Free and infected races of *L. perenne* were also studied and transmission by the female parent was found in suitable crosses.

The fungus, which is present in tiller buds and leaves, was distributed by vegetative propagation of infected plants.

N. J. G. SMITH and F. B. POPE. The Association between the Gasteromycete *Polysaccum* and *Eucalyptus* Roots.

In the Eastern Cape *Polysaccum crassipes* seems invariably to occur under *Eucalyptus* trees, although in the Western Cape we have seen it under *Leptospermum* and Bruns\* found it under pines in Europe.

The hot sandy soil of the Cape frequently contains rhizomorphs of no other fungi. *Polysaccum* mycelium, moreover, is usually yellow and is easily traced. Its mode of life is various: a saprophytic life in the soil is followed by some hyphae, others live on or among the bark layers of living roots, as noted by Van der Bijl†; sometimes the fungus is parasitic or it may form mycorrhiza. That both of these last-named relations can exist in different branches of the same root is most interesting.

The parasitic condition involves a free spread of inter- and intracellular hyphae, accompanied by the death of root cells. The invasion is not confined to the outer cells but penetrates deep into the xylem. Parasitised roots are thin, but old enough to have a corky covering. Younger roots, that are still in the absorptive stage, become mycorrhizal, and show yellow coraloid clusters of much the same form as Melin's‡ racemose mycorrhiza of spruce.

All the main internal features (the layered fungus mantle, the palisade-like epidermal cells with "Hartig-net" mycelium) are paralleled in Melin's descriptions of other tree mycorrhiza. The fungus is usually present inside the cells of the epidermal layer and the outermost cortical layer but rarely occurs in any deeper layer. Intracellular digestion of hyphae is exhibited with a clarity unusual in tree mycorrhiza.

The fungus grows best on agars made with a decoction of *Eucalyptus* roots but even on these it does not grow very well so that experiments on the inoculation of roots with pure-culture mycelium have not progressed far.

W. H. WILKINS. Preliminary account of the parasitism of *Ustulina vulgaris*.

The amount of rot present in an infested lime and a beech was described and a summary given of the author's introductory paper (*Trans. Brit. Mycol. Soc.* xviii (1934), 320-46).

\* Bruns, E., "Beitrag zur Kenntniss der Gattung *Polysaccum*," *Flora*, lxxviii (1894), 67-75.

† Van der Bijl, P. A., "Note on *Polysaccum crassipes* D.C.: a common fungus in *Eucalyptus* plantations round Pretoria," *Trans. Roy. Soc. S. Africa*, vi (1917), 209-14.

‡ Melin, E., "Experimentelle Untersuchungen über die Konstitution und Ökologie der Mykorrhizen von *Pinus silvestris* L. und *Picea Abies* (L.) Karst.," *Falck. Mykol. Unters. und Berichte*, ii (1923), 73-331.

## REVIEW

*Die Pilze Mitteleuropas. Band I. Die Röhrlinge*, by F. KALLENBACH.  
 Lief. xii. Pp. 79-86. Pls. 30, 31. Leipzig, Werner Klinkhardt,  
 1934.

The previous part of Kallenbach's Monograph was published in 1930 and mycologists had begun to fear that the work would never be completed. The remaining parts are promised at six-monthly intervals. Meanwhile Band II is announced to begin this year and will deal with *Lactarius* (B. Knauth) and the Tremellineae (W. Neuhoff). It is to be hoped that the revised time-table can be kept to for it is eight years since the first part of the *Boletus* monograph appeared. There can be no doubt that it will be the standard work on the genus for many years to come, but most students would have preferred to have a complete though expensive volume now rather than parts in paper covers appearing at odd intervals over such a number of years. We trust that the publisher has most of the material for the next volume in hand before he begins publication.

The present part of the *Boletus* monograph has two coloured plates and eight pages of text.

The first plate shows most excellent representations of the fungus usually called *Boletus erythropus* but to which the name *B. miniatoporus* Secr. is given. Persoon used the specific epithet *erythropus* for the species which is now most frequently called *B. Queletii*. Fries adopted Persoon's name only, first applying it to the fungus figured here, in 1818, giving it specific rank, but reducing it to varietal rank (var. of *B. luridus*) in the *Systema*. The International Rules start from this work and so unfortunately it means that we shall have to take the first specific name after Fries: it looks as if this is *B. perniciosus* Roques.

A key is provided to the species of *Boletus* with reddish orifices to the pores. These species were all figured conveniently on Plate 2: *B. Satanus*, *B. rhodoxanthus* = *purpureus*, *B. erythropus* = *Queletii*, *B. miniatoporus* = *erythropus*, and *B. luridus*. The first essential to a better understanding of the genus is well on its way, i.e. the clear definitions of the species—the precise nomenclature can wait awhile.

The second plate figures *B. appendiculatus*. It is perhaps printed a little too reddish brown as the author states but the fact that he has chosen to comment upon this shows the general excellence of the plates.

J. R.

## A LUMINOUS AGARIC (*PLEUROTUS SP.*) FROM SOUTH BURMA

BY S. R. BOSE

(Professor of Botany, Carmichael Medical College, Calcutta, India)

(With 3 Text-figures)

PIECES of luminous wood were obtained from Tenasserim in South Burma in August 1931, and August 1933, through the kindness of Mr P. T. Russell, Superintendent of the Cinchona Cultivation in South Burma under the Botanical Survey of India. In October 1932, from the same place, other pieces were obtained through the kindness of Mr K. P. Biswas, Curator of the Botanical Gardens Herbarium, Shibpur, on a collecting tour to South Burma. The wood belonged chiefly to dead stumps of *Lagerstroemia* sp. (Lythraceae) and *Pentace burmannica* (Tiliaceae). The luminosity had almost failed when the wood reached my hands at Calcutta. The pieces were at once wrapped with moist cotton-wool and kept in a tray with a little water. The light increased in the course of a few days, and a number of tiny fructifications of a *Pleurotus* developed on some of them in the course of a month. The fructifications were luminous all over, that is to say, the stalks as well as both surfaces were equally luminous. The vegetative mycelium in the wood giving rise to these fructifications was also luminous; hence pieces of wood infected with fungal hyphae looked very bright in the dark. In this respect the fructifications differed from those in Buller's list<sup>(4)</sup> of twelve luminous species of *Pleurotus*, in which only the fruit body is luminous.

Since the *Pleurotus* examined does not exactly agree with the descriptions of luminous species from Australia, the Philippine Islands, Japan and America (*P. candescens* F.V.M., *P. Gardneri* Berk., *P. illuminans* F.V.M., *P. Lampas* Berk., *P. nidiformis* Berk., *P. phosphoreus* Berk. (= *P. olearius* DC.), *P. japonicus* Kaw., *P. facifer* B. & C., *P. igneus* Rumph., *P. noctilucens* Lév. and *P. Prometheus* B. & C.), a detailed description of the species is given with figures of its two surfaces (Figs. 1 and 2).

Pileus: Kidney-shaped with centre depressed, 10 x 8 mm., quite smooth, of pale tawny colour turning to white at the margin, upper surface marked with fine radiating anastomosing lines. Margin involute, flesh thin.

Stalk: Lateral, 8 mm. long, white, dilated above, quite smooth, solid and rigid.

Hymenial surface: Pure white, gills decurrent, edge entire, tramal hyphae running divergently parallel.

Basidia:  $12-16 \times 6-8 \mu$ . Spores white, oval,  $2-3 \times 4-5 \mu$ . Cystidia none. Fructifications usually do not revive in moist condition when once fully dried.

From a spore print on a sterilised clean glass slide a number of spores were removed aseptically to tubes of malt-extract agar kept at room temperature in diffused light. In three to four days fine white mycelium developed and covered the slants in a further period



Fig. 1. Upper surface of luminous  
*Pleurotus* sp.



Fig. 2. Hymenial surface of luminous  
*Pleurotus* sp.

of ten days. Several subcultures were grown on sterilised bread media in Petri dishes, tubes and Erlenmeyer flasks, and on sterilised potato slabs within Roux tubes and on sterilised blocks of the luminous wood within Roux tubes, with a little water at the constricted end. Tissue culture from a clean piece of the sporophore was also successful in bread as well as in malt-extract agar medium. In liquid media of 1 per cent. peptone and 2 per cent. glucose the growth was mostly submerged, the colour of the media changing to brownish in the course of time.

The mycelium in these artificial cultures, as long as it is pure white, gives out a soft greenish light. A spectroscopic analysis of the emitted

light kindly carried out by Dr P. Krishnamurtti, with the help of a quartz spectroscope, under the direction of Prof. Sir C. V. Raman, F.R.S., shows that the rays are mostly in the greenish region—5400–5000 Å. When the white mycelium becomes brown, in thirty to forty days, in culture flasks and tubes, it no longer gives out any light. The browning of the white hyphae occurs in patches and it takes a long time (about two months) to become uniform deep brown all over the cultures. The luminosity in artificial cultures has been kept more than two years by continual subcultures in fresh bread media. Wounding the mycelium with a sterilised needle at once



Fig. 3. Fructification in artificial culture on sterilised luminous wood block within Roux tube (portion of the tube shown).

increases the luminosity and causes fresh growth of young white hyphae over the old ones. In bread media in flasks the hyphae ultimately exude copious drops of white liquid which gradually turn brownish to black. In older cultures the hyphae form compact strands here and there, and clamp connections are abundant. In this condition the hyphae become submerged and form brownish patches here and there; here also only the white areas give out light. Fructifications have not yet appeared in these bread media during these two years, but on sterilised wood blocks tiny white fructifications appear in six to eight months (Fig. 3). The best vegetative growth takes place in sterilised bread media and in potato slabs at room temperature.

Bothe's (3) experience with the culture of luminous *Mycena tintinnabulum* was almost the same except that the light of his specimen was white and not greenish, and that he could not get any fructification in artificial culture.

The effect of sunlight on the luminosity of the fungus was tested by exposing the hyphae within the culture vessels directly to the rays of the sun by removing the cotton plugs. Closed vessels were also exposed to the sun. Increase in luminosity, usually of a temporary nature, was observed only when the hyphae had been directly exposed to the sun's rays. Luminosity did not fail entirely even when a culture on bread medium was kept in entire darkness for a month and a half. On the other hand light could develop well in the course of a month in a flask inoculated with the luminous mycelium, though it was kept in total darkness in an incubator at 22° C. This shows that luminosity here is continuous and quite independent of previous illumination of the fungus, as has been remarked by Harvey (6), pp. 68-9) in bacteria and fungi in general. In this respect there is a great difference from the behaviour of the luminous wood (of *Sterculia* sp.) that I (2) received from Buxa Duars in Jalpaiguri (Bengal) in September 1929. There the luminescence was distinctly intermittent, depending on the general stimulation of the living hyphae in the presence of the sunlight; Perkins's (10) experience with the light of glowworms, which glow only by night, was almost the same. He concluded that external light was probably not needed for storage on the lines of chemical phosphorescence but necessary to stimulate natural conditions. Unfortunately, light did not develop in cultures (on a bread medium) of the fungus from the luminous wood of Jalpaiguri; neither could the fungus be identified, since the cultures never fruited but continued long in the vegetative condition, as did the mycelium X of Molisch (9).

No satisfactory explanation can be given as yet of the utility of the luminosity to the fungus itself. On the other hand there is every chance that the glow of light in the dark may attract a number of insects or mites which may cause injury to the fungus. Recently, Gurwitsch (5) and his collaborators have reported emission of invisible mitogenetic rays falling in the ultra-violet region of the spectrum from a great variety of cells and tissues; according to them the most powerful source of radiation appears to be the material which is in a high state of mitotic, metabolic, nervous or mechanical activity. Potozky and Braunstein (11) claim that in a variety of chemical oxidations ultra-violet light of the same wave-length as the mitogenetic rays of Gurwitsch may be produced. The luminescence of the fungus described here depends largely on the access of oxygen, but in contrast to Gurwitsch's radiation the rays are mostly in the greenish region of the spectrum.

Attempts to extract enzymes in luminous condition from the mycelia, using Harvey's methods(6), were unsuccessful. Neither did the mixing together of extracellular and intracellular enzymes produce any light in the solution.

The response of the luminous *Pleurotus* to oxygen, hydrogen, nitrogen and carbon dioxide was the same as that of luminous leaves and stalks from different parts of Bengal(1).

Subsequently, in November and December 1933, I obtained from Khandala, Bombay, pieces of dead wood, containing fungal hyphae sent four months after collection by Mr K. J. Kabraji of the Poona Meteorological Department, Bombay. Luminosity had almost disappeared when the pieces of wood reached me, but could be revived after soaking with distilled water for two or three days. I am told that such luminous twigs are very common on the slopes of the Western Ghats of the Bombay Presidency, particularly the Umri hilltop at about 2000 ft. elevation. Sterilised bread media in flasks were at once inoculated with a small piece aseptically removed from the inside of the luminous twigs. Subcultures in the same medium gave pure white growth of the mycelium fully covering the outer surface of the bread in the course of a week. Subcultures have also been started on sterilised pieces of luminous twigs within Roux tubes with a little water at the constricted end. Light has not developed as yet in these artificial cultures; neither has any fructification appeared. Consequently the identity of the fungus causing the luminosity has not been established. Direct exposure to sunlight increases the luminosity of the luminous twigs, as in luminous wood of *Sterculia* reported from Buxa Duars(2).

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## OBSERVATIONS ON *FOMES POMACEUS* (PERS.) BIG. & GUILL. INFECTING PLUM TREES

BY EILEEN FISHER  
(*Botany School, Cambridge*)

(With 4 Text figures)

PLUM trees growing in Cambridgeshire are frequently attacked by the fungus *Fomes pomaceus* (Pers.) Big. & Guill. Although the variety Pershore is generally most susceptible, on one plantation at Histon a large number of trees belonging to the variety Victoria were found to be heavily infected.

### REVIEW OF PREVIOUS WORK

Although the literature concerning wood-rotting fungi is so extensive, *Fomes pomaceus* seems to have escaped the attention of most investigators. Baxter<sup>(1)</sup> has studied a resupinate form of *F. pomaceus* occurring chiefly on *Crataegus*, but also on *Prunus americana*; and this is the first record of any cultural study of the fungus.

Owing to the similarity of decay produced by *Fomes pomaceus* and by *F. igniarius* (Linn.) Fr., special attention has been paid to references concerning the latter species.

With both of these fungi a "gumming" of the wood in the early stages of decay is followed by a "white-rot." The general opinion of those who have studied these species seems to be that the "white-rot" is due to delignification of the wood, although this suggestion is not supported by those investigators who have tackled the problem from a chemical standpoint.

More recently Campbell<sup>(4, 5)</sup> has made a chemical examination of several kinds of "white-rot," and he has shown that the characteristic feature of this type of decay concerns the pentosan constituents of the wood, and that some lignin may remain even after the development of the typical white colour.

In 1878, Hartig stated that the delignifying action of *Polyporus igniarius* was first directed towards the inner part of the wall of the wood fibres, dissolution of the resulting cellulose layer following later.

Spaulding<sup>(17)</sup> found "an inner supernumerary layer of cellulose" lining the healthy wood fibres of *Populus tremuloides*, while in wood infected with *Fomes igniarius* removal of this cellulose layer preceded delignification of the middle lamella region.

In 1909, von Schrenk and Spaulding stated that one of the principal effects of *Fomes igniarius* on the wood of the host was "solution of the lignin elements of the cell wall."

However, by chemical analysis of aspen wood infected with *F. igniarius*, Johnson and Hovey<sup>(12)</sup> have since shown that it is the cellulose rather than the lignin constituent of the wood which is attacked by this fungus.

In 1925, Baxter included in his study of the "hard-wood heart-rotting fungi" both *F. igniarius* and a strain of *F. pomaceus*. From microchemical tests he concluded that both these fungi had a delignifying action on the elements of the wood, and that the decay produced by *F. igniarius* might be distinguished by the development of black lines limiting the infected zone.

#### OBSERVATIONS ON THE GERMINATION AND LONGEVITY OF THE SPORES

An inspection was made of infected plum trees growing at Meldreth, Cambridgeshire, at approximately monthly intervals from November 1931 to May 1932.

Fructifications of the fungus were gathered throughout this period, and spore deposits were obtained in the laboratory by suspending the fruit bodies over sterile microscope slides. After about twenty-four hours a thick white deposit of spores was usually obtained in this way.

White<sup>(19)</sup> from observations on spore deposits collected in the field from fructifications of *F. applanatus* found that spore discharge, which began in early spring, was brought to an end by heavy frosts in late autumn. However, he obtained spore deposits from detached fructifications during the winter, and this he attributed to loss of surface adhesion on the part of spores lodged in the pores.

In the present investigation the most copious spore deposits of *F. pomaceus* were obtained from fructifications collected during the last week of November, although scanty deposits were obtained throughout the winter. The spore-covered slides were kept in a closed box and the germinability of the spores was tested from time to time. For this purpose a spore suspension was made in sterile tap water. This was then painted with a camel-hair brush over a film of Dox's agar on a slide, which was kept in a sterile Petri dish. Microscopic examination of the spores was made each day. This method, which proved very satisfactory for studying spore germination, is essentially the same as that used by Hirt<sup>(11)</sup> in his study of *Polyporus gilvus*, but it was found that the use of slides facilitated microscopic examination. Vernon<sup>(18)</sup> has described a method for studying fungal

growth microscopically, in which the fungus is grown under a cover-slip, and the medium takes the form of a small disc of agar. This method proved unsatisfactory for *Fomes pomaceus*.

The latent period of germination in these spores seems to be long, as in no case was any sign of activity noticed for at least seventy-two hours. White<sup>(19)</sup> and Hirt<sup>(11)</sup> found this period to be much shorter for spores of *F. appplanatus* and *Polyporus gilvus* respectively; in these latter fungi, water alone was sufficient to induce germination of the spores of *Fomes pomaceus*, and a nutrient medium, which Buller<sup>(3)</sup> found necessary with spores of *Polyporus squamosus*, was not required. The first visible stage of this process was the development of a single unbranched non-septate germ tube, followed within approximately twenty-four hours by the appearance of a second germ tube arising from the opposite end of the spore.

It was found in this way that some spores of *Fomes pomaceus* retained their germinability for a period of twenty-four weeks.

#### CULTURAL STUDY OF THE FUNGUS

Cultures were obtained from spores of *F. pomaceus*, and the cultures isolated from decayed wood were compared with them and found to be identical.

Isolations from diseased wood were made in the following manner: A length, approximately 2-3 in., of a diseased branch was chiselled into small triangular segments. By passing the wood segment through a flame the surface was sterilised, and then shavings, cut with a sterile razor from the junction of decayed and healthy wood, were plated out on to a nutrient medium such as prune agar. About five days later, fungal colonies developed, which after subculturing on to plain agar were transferred to tubes containing some suitable nutrient medium. Sterilised plum wood blocks formed a very convenient medium for the growth of the fungus. The medium used seemed to have little effect on the type of growth, which remained the same on malt agar, Dox's agar, and plum wood blocks. The mycelium is of a woolly nature due to dense development of aerial hyphae, and is colourless in the early stages of its growth, but later darkens to "cinnamon buff" (Ridgway<sup>(13)</sup>).

In *F. pomaceus* forma *Crataegi* isolated by Baxter<sup>(1)</sup> the mycelium is apparently darker in colour, and when grown on malt extract agar it becomes "cinnamon brown" and later "snuff brown" (Ridgway).

The mycelium of *F. pomaceus* retains its vitality for a long time, a fresh culture having been established from one on a plum wood block after three and a half years.

EFFECT OF THE FUNGUS ON PLUM WOOD

Examination of the cut surface of badly infected branches revealed a white crumbling mass in the central region of the heart-wood, separated from the outer healthy wood by a brown "gummy" zone (Fig. 1 A). In some specimens the "gummy" and the more advanced stage of decay or "white-rot" alternated, as illustrated in Fig. 1 B.

Microscopic examination was made of the wood from healthy, "gummy," and "white-rot" zones respectively. Sections of the last two zones, stained with safranin and picro-aniline blue (Cartwright(6)), or with safranin and light green, clearly showed fungal hyphae, which were absent from the healthy wood (Fig. 2).

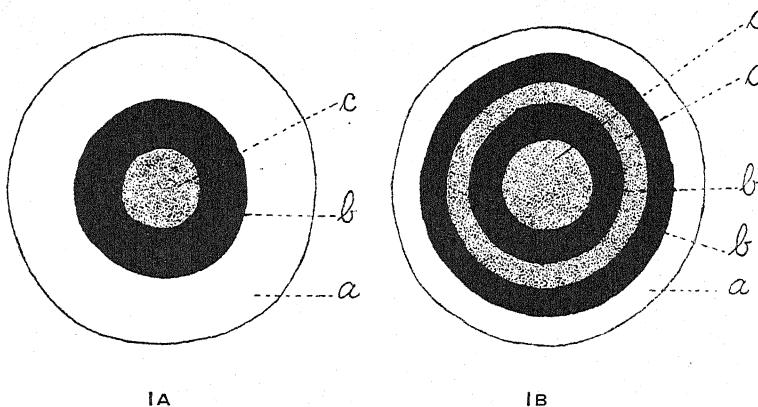


Fig. 1 A and B. Diagrams illustrating the appearance of the wood of the cut ends of two plum branches infected with *Fomes pomaceus*. a, zone of healthy wood; b, "gummy" zone; c, "white-rot" zone.

From macroscopic observation, it is evident that in the early stage of decay the wood remains quite firm and may be distinguished from that in the healthy condition only by its brown colour, due to the accumulation of large quantities of gum in the vessels and medullary-ray cells. From a comparison of sections from healthy and "gummy" regions, treated with iodine, the development of gum in the latter would appear to be connected with the disappearance of starch from the medullary-ray cells. This is contrary to the observations by Hartig(10) on the effect of *Polyporus igniarius* on oak wood, for he found the disappearance of the starch grains to be deferred until after the removal of the lining layer of the fibres. On the other hand, my observations support the theory of gum formation put forward by

Brooks and Storey<sup>(2)</sup> in connection with silver-leaf disease of plum trees caused by *Stereum purpureum*.

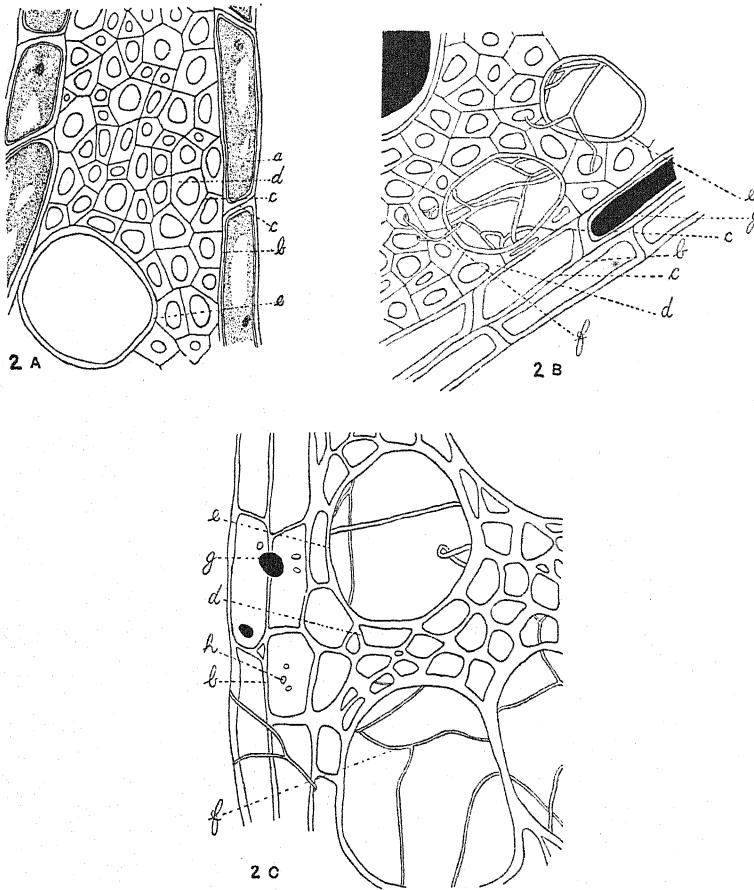


Fig. 2. Transverse sections of plum wood infected with *Fomes pomaceus*.  $\times 312$ . Stained with safranin and picro-aniline blue. A, healthy zone, showing thick-walled wood fibres and protoplasmic contents of the medullary-ray cells. B, "gummy" region, showing fungal hyphae and large quantities of gum. C, "white-rot" zone, showing thinner-walled fibres and empty medullary-ray cells. a, protoplasmic contents of medullary-ray cell staining blue; b, wall of medullary-ray cell; c, middle lamella; d, wall of fibre; e, wall of vessel; f, fungal hypha staining blue; g, gum; h, simple pit. The walls of the wood elements take up the safranin stain throughout, especially in the middle lamella.

Microscopic examination revealed that the more advanced stage of decay, when the wood becomes white and soft, is characterised not only by a disappearance of gum but also by reduction in thickness of the fibre walls.

Harlow(8, 9) has drawn attention to the unreliability of microchemical methods as a means of cell-wall analysis; and Hirt(11) in his investigation of the decay caused by *Polyporus gilvus* regarded results derived from staining reactions as significant only when supported by chemical analysis.

In the present investigation, which was completed in Australia, the amount of decayed wood available was limited, so it was not possible for a chemical analysis to be made. However, some indication of the changes taking place can be ascertained by reviewing the results of some of the more reliable microchemical tests when applied to healthy and decayed wood.

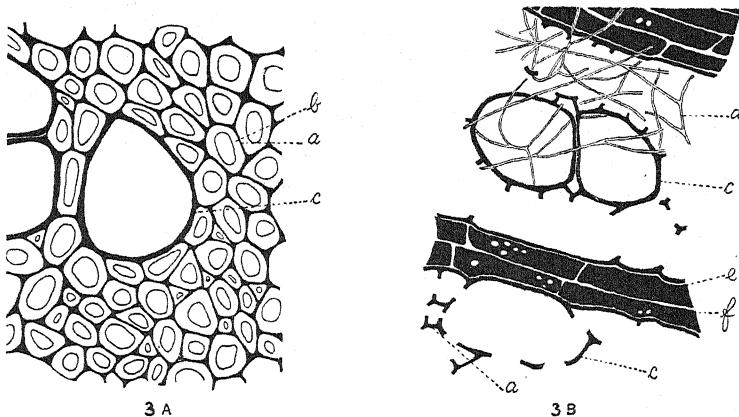


Fig. 3. Transverse sections of plum wood. Stained with safranin and light green. A, healthy wood showing differentiation of fibre wall into two distinct layers.  $\times 312$ . B, wood in advanced "white-rot" stage of decay caused by *Fomes pomaceus*.  $\times 188$ . a, middle lamella of fibre wall staining red; b, lining layer of fibre wall staining green; c, wall of vessel staining red throughout; d, fungal hypha staining green; e, wall of medullary-ray cell staining red throughout; f, simple pit.

Sections of healthy wood stained overnight with 1 per cent. safranin in 50 per cent. alcohol, and counter-stained with light green for thirty minutes, showed clearly that the fibres were provided with a thick lining layer which stains green. This is apparently quite distinct in its constitution from that of the middle lamella of these elements, and from the entire wall of the other elements, vessels and medullary-ray cells, which take up the safranin stain (Fig. 3 A).

The application of phloroglucin and hydrochloric acid resulted in a similar differentiation of the fibre wall into two distinct layers; (i) the middle lamella, giving a bright pink reaction, which was absent from (ii), the thicker lining layer. The same pink coloration was produced in the wall of the vessels throughout its thickness, and

in the medullary-ray cells the middle lamella appeared as a clear-cut pink line in the central region of the rather lighter stained general cell wall (Fig. 4).

The same cell wall layers again became differentiated when wood sections were treated with aniline sulphate and sulphuric acid, but here the colour reaction was golden yellow. As pointed out by Crocker (7) it has been shown that these two latter colour reactions are due to aldehydes, mainly coniferyl aldehyde, which accompany the lignin.

The Mäule reaction is another very generally used test for lignin, and it is recommended by Schneider and Zimmermann (15) for use in

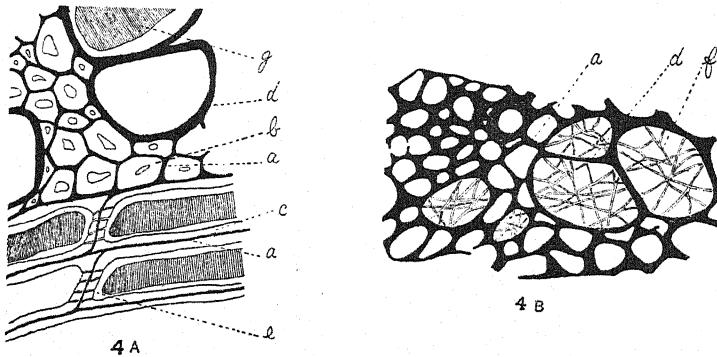


Fig. 4. Transverse sections of plum wood infected with *Fomes pomaceus*.  $\times 312$ . Stained with phloroglucin. A, "gummy" region, showing the lining layer of the wall of the fibres and abundance of gum. B, "white-rot" stage of decay, in which the pink-staining skeleton formed by the middle lamellae of the fibres and vessels is infested with fungal hyphae. a, middle lamella of fibre wall, stained bright pink; b, lining layer of wall, unstained; c, wall of medullary-ray cell, stained faintly pink; d, wall of vessel, stained bright pink; e, simple pit; f, fungal hypha; g, gum.

conjunction with the phloroglucin test and as complementary to it; the colour reaction is dependent on a portion of the lignin molecule which is distinct from the chemical grouping responsible for the pink coloration with phloroglucin. Sections of healthy wood were placed in a 1 per cent. potassium permanganate solution for five minutes, then after washing with water and dilute hydrochloric acid for one to two minutes, application of a drop of ammonia produced a deep red coloration throughout the entire wall of all elements of the wood. The lining layer of the fibres did not become differentiated from the middle lamella as when treated with phloroglucin.

In view of this evidence it seems impossible to consider the lining

layer of the fibres as consisting of pure cellulose\*, although sections treated with chlorzinc-iodine indicate that this compound is present in considerable quantity, as is shown by a definite blue coloration in this region. The middle lamella of the fibres and the entire wall of the vessels show no colour change at all; similarly the middle lamella of the walls of the medullary-ray cells remains unchanged, but the other parts of these walls are stained faintly blue.

Spaulding (17) used only the phloroglucin and chlorzinc-iodine tests when he described an "inner supernumerary layer of cellulose" in the wall of the wood fibres of *Populus tremuloides*.

That other substances in addition to cellulose take part in the constitution of this lining layer in plum-wood fibres at least is also indicated by the effect on it of various cellulose solvents. The action of (i) 72 per cent. sulphuric acid, (ii) ammoniacal cupric oxide, and (iii) zinc chloride dissolved in twice its weight of hydrochloric acid, was tested on sections of healthy wood, and in every case this layer of the fibre wall remained apparently unaltered, even when the sections were left soaking in the solvent for some days.

From these microchemical tests it would appear that, in healthy plum wood, the walls of the tracheae are of uniform composition, but in the fibres the lignin is more concentrated in the region of the middle lamella where it is accompanied by certain aldehydes, while in the remainder of the fibre wall the cellulose content is higher and the aldehydes usually associated with lignin are absent. In the medullary-ray cells the lignin and its associated aldehydes appear to be concentrated in the middle lamella region, the remainder of the cell wall being slightly richer in cellulose as is shown by the action of chlorzinc-iodine, although the blue colour reaction is not nearly so intense as that produced in the fibres.

Sections of plum wood infected with *Fomes pomaceus* were subjected to the above-mentioned microchemical tests and compared with those of healthy wood.

In the early "gummy" stage of decay the walls of the woody elements apparently remain unaltered, the only visible change in the wood being an accumulation of large quantities of gum, accompanied by the disappearance of starch from the medullary-ray cells.

Of the decay in the later "white-rot" stage, the outstanding

\* Ritter (14), presumably from this portion of the cell wall, has isolated partially a second type of lignin which he termed "cell wall" lignin. Harlow (8, 9) attempted to confirm Ritter's results "but in no case could conclusive evidence be found of the presence of 'cell wall' lignin," and Harlow has suggested that this substance might be a mixture of "middle lamella" lignin and a certain amount of unhydrolysed cellulose.

In (8) Harlow has questioned the reliability of the Mäule reaction for purposes of microchemical analysis, attributing the red colour developed in the secondary cell wall to spreading of the "lignone chlorides" from the middle lamella.

feature was the removal of the lining layer from the wall of the fibres, leaving a framework in which the so-called "lignin colour reaction" was readily induced by the application of phloroglucin and hydrochloric acid (Fig. 4). This stage of decay appears also to be characterised by the disappearance of the gum which accumulated in the early stages of infection, leaving the medullary-ray cells quite empty, so that the simple pits on the walls of these cells become clearly visible (Figs. 2 C and 3 B).

It has been stated by Baxter (1) that in wood decay produced by the strain of *F. pomaceus* studied by him, the walls of the medullary-ray cells are the last to be attacked by the fungus. Observations made during the present investigation lend support to this contention. In transverse sections of plum wood in the final stages of decay, the medullary-ray cells were observed forming radiating plates, which were conspicuous even when the framework of the other woody elements showed signs of disorganisation (Fig. 3 B). Also, comparison of sections taken from "gummy" and "white-rot" stages of decay respectively showed the increase in hyphal development in the latter stage to be most manifest in the medullary rays. On the other hand, von Schrenk and Spaulding (16) have found that with *F. igniarius* it is in the earlier stages of decay that the hyphae develop abundantly in the medullary-ray cells.

Plum wood in the final "white-rot" stage of decay was found to be very densely infested with fungal hyphae, which indeed formed the most striking feature when sections of such wood were examined microscopically. The hyphae become finer as decay proceeds, and this fact, which has also been noted by Hartig (10) and Buller (3) in *Polyporus igniarius* and *P. squamosus* respectively, is attributed by them to lack of oxygen and starvation of the fungus.

Softening of the wood in the "white-rot" stage of decay produced by *Fomes pomaceus* and by *F. igniarius* has been attributed by the majority of investigators to delignification. Evidence derived from the present investigation on the effect of *F. pomaceus* on plum wood does not substantiate this suggestion, as in the most advanced stages of decay the remaining skeleton of woody tissue still gave a positive reaction when lignin tests, such as phloroglucin and Mäule's method, were applied. The characteristic softening of the wood appears to be due rather to the removal of the layer lining the fibres. In so far as an accurate analysis can be made from the microchemical methods used, these fibres may be regarded as lignified, although devoid of the aldehydes which usually accompany lignin, and as being rich in cellulose. This conclusion is in agreement with the observation, made from chemical analyses by Johnson and Hovey (12), that *F. igniarius* attacks the cellulose rather than the lignin constituents of aspen wood.

#### INOCULATION EXPERIMENTS

During the last weeks of 1931 and the early part of 1932 a number of Victoria and Pershore plum trees were inoculated with *F. pomaceus*. Some of the trees were growing in the open at the Botanic Garden, and others in a greenhouse at the University Farm, Cambridge.

These experiments were carried out on branches about  $\frac{1}{4}$ – $\frac{1}{2}$  in. in diameter with (i) spores, (ii) actively growing mycelium. In the first method a spore suspension in sterile water was made, and this, applied by means of a sterile pipette to the freshly cut end of the twig, was drawn into the wood vessels. In the second method each mycelial inoculation was made by means of a *T*-shaped incision in the stem of the tree. After the introduction of the organism and moistening with sterile water, the wound was bound up with thick black wool. Control experiments using sterile water were also made.

Unfortunately, this study of the pathogenicity of *F. pomaceus* on plum trees was terminated rather prematurely by my return to Australia, about six months after the inoculations were made. Some of the inoculated twigs were cut and examined, and although the fungus had not grown sufficiently during this period to make any accurate observations, the consequent browning of the wood appeared to extend further in the variety Pershore than in Victoria.

In March 1933, that is approximately fifteen months after the inoculations were made, those twigs which had not already been removed earlier, were cut and examined by Mr Brooks. At the end of this period branches inoculated with mycelium showed very slight spread of the fungus, and the browning of the wood extended at most for 1 in. above and 1 in. below the point of inoculation, with only one exception, a twig from a Pershore tree in which the wood exhibited discoloration for 2 in. above and 4 in. below the inoculation point. Inoculation by means of a spore suspension resulted for the most part in death of the "snag" only, *i.e.* the portion of the twig extending from its cut surface down to the nearest node below, which dies inevitably without inoculation. In two instances, however, death of the twig inoculated with a spore suspension extended below the snag; in one of these, on a Victoria tree, death extended for 2 in., while in the other, on a Pershore tree, it extended for 4 in. below the snag.

It may be concluded therefore that under the conditions which prevailed during the course of these experiments, *F. pomaceus* is only very feebly parasitic on plum trees, and that the variety Pershore is rather more susceptible than the variety Victoria. In plum plantations usually only old trees are attacked by this fungus and the progress of the disease is generally slow. In the experiments described

above it was only possible to inoculate comparatively young branches. Perhaps inoculations of older wood would have indicated a more rapid spread of the fungus.

#### SUMMARY

1. The incidence of *F. pomaceus* on plum trees in the Cambridgeshire district is noted.
2. Attention is drawn to the similarity in the type of wood decay produced by *F. pomaceus* and *F. igniarius*, and an outline of the results of previous investigations on these two fungi is given.
3. Spores of *F. pomaceus* are sometimes capable of germination twenty-four weeks after liberation from the sporophores.
4. Isolations of *F. pomaceus* have been made from decayed wood, and these cultures are found to be identical with those grown from spores.
5. The cultural characters of the fungus are noted and compared with those of the strain isolated by Baxter.
6. The fungus is very resistant to desiccation; a fresh culture was obtained from one that was three and a half years old.
7. A study of the effect of the fungus on plum wood has been made, using microchemical methods.
8. The copious gum formation which is so characteristic of the early stages of decay is associated with removal of starch from the medullary-ray cells.
9. The characteristic feature of the later "white-rot" stage is not a delignification of the woody elements, as was formerly supposed, but the removal of the thick lining layer from the walls of the wood fibres.
10. This internal layer of the wood fibre wall is rich in cellulose, but devoid of the aldehydes which usually accompany lignin.
11. The last walls of the wood elements to be attacked by the fungus are those of the medullary-ray cells.
12. Healthy Pershore and Victoria plum trees have been inoculated, using both spore and mycelial inocula. The results of the inoculation experiments indicate that *F. pomaceus* is only feebly parasitic on plum trees, the variety Pershore being slightly more susceptible than the variety Victoria.

This investigation was suggested by and conducted under the direction of Mr F. T. Brooks, to whom I should like to express my gratitude for advice and help.

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## EXPERIMENTS ON FINGER-AND-TOE DISEASE (*PLASMODIOPHORA BRASSICAE*)

By GEO. POTTS, B.Sc., Ph.D.  
(*Grey University College, Bloemfontein, South Africa*)

THE work here described was conducted at Newcastle-on-Tyne and Halle-an-der-Saale, in the Departments of Prof. M. C. Potter and the late Prof. G. Klebs respectively, from both of whom valuable help was received.

Part of the article was read before the British Association at their meeting in Johannesburg in 1905 and appeared in abstract in their *Report* for that year, but, owing to a revival of interest in the disease and a request for further details of the experiments, it seems opportune to publish a fuller account.

Most of the experiments were performed in pots, though for a few of them small plots were used. With pots, the material used was carefully mixed before potting; and in the plots, the soil, to a depth of about nine inches, of the whole area to be covered by an experiment was dug up, thrown into a heap, mixed and put back. Similarly, the infective material was carefully crushed (or chopped) and mixed before being used for inoculation.

In the earlier experiments the turnip, on account of its importance as a farm crop, was the plant chiefly grown, but experience led to its replacement by mustard, and to duplicating this with candytuft, which is much less liable to attacks by aphides and flea beetle.

Owing to their rapid growth, several successive crops of mustard and candytuft can be grown in a single season, and there is thus an opportunity of immediately repeating experiments. Turnips, on the other hand, require a whole season to mature. Mustard and candytuft have the further advantage of requiring very little space, so that larger numbers can be grown to maturity on a small area without serious overcrowding.

### SPECIES ATTACKED

The disease has been recorded in most of the genera of Cruciferae. Judging by the proportion of plants attacked, I found the following very susceptible to the disease: candytuft, mustard, *Sisymbrium*, wall-flower, and the numerous cultivated species of *Brassica*.

In an experiment at Halle on ground on which the disease had not been known to occur, spores from diseased swedes and turnips produced the disease in *Isatis* (5 attacked out of 20), *Cochlearia* (10 out

of 40) and *Sisymbrium* (27 out of 30), but not in *Draba*, *Erysimum*, *Hesperis*, *Matthiola*, or *Raphanus*, although the disease has been recorded for all these genera. Halsted (1896) had a somewhat similar experience with *Matthiola*. More recent work on the susceptibility of various Cruciferous plants to attack by *P. Brassicae* will be found in the publications of Gleisberg (1923), Gibbs (1932) and Rochlin (1933).

The disease has not been reported outside the Cruciferae, and attempts were made to infect certain plants nearly related to that family, or those having a similar ash composition (Wolff, 1871), but with negative results. The following were the species tested: *Reseda odorata*, *Corydalis glauca*, *Fumaria officinalis*, *Allium schoenoprasum*, *Urtica pilulifera*, and *Spinacia oleracea*.

#### THE INJURY DONE BY *PLASMODIOPHORA* TO ITS HOST

The extent to which attacked plants suffer from the disease varies with the species, but depends also on the age of the plant when it first becomes infected. Plants, of whatever species, when attacked late in life suffer comparatively little direct injury; but if attacked while still young certain species suffer severely, and either succumb or remain much stunted, whilst other species are apparently not injured by the disease. Turnips, charlock, *Sisymbrium* and wallflower suffer severely, and plants attacked when young show obvious symptoms of general ill-health apart from the tumours. Mustard, candytuft, garden cress and horse-radish, on the other hand, are apparently uninjured in general health, and the presence of disease cannot be detected without examining the roots.

The wallflower when attacked young, usually succumbs speedily, but if it survives, the seat of attack does not become a tumour but dries and splits.

If a section be cut through the root of a young diseased turnip it will be found that the disturbance of the vessels is very great, pieces being forced from the vertical into oblique and even horizontal positions (Kühn, 1858; Wakker, 1892). A detailed examination leaves the impression that the continuity of the vessels is broken to such an extent as to interfere seriously with their water-conducting function. This, no doubt, causes the well-known symptom of wilting of the leaves in turnips.

When turnips are attacked young the centre of disease is near the vessels which are disturbed by the cell multiplication and enlargement induced by the parasite. On the other hand, when infection is delayed, the seat of the tumour is superficial, and so far removed from the vessels that they are not seriously disturbed. Hence,

turnips attacked late in life show comparatively little indication of general ill-health.

A microscopic examination of diseased roots of two species that apparently are not directly injured by attack, showed that the vessels are situated in a hard fibrous strand, running down the centre of the root, and are not disturbed by the cell multiplication and enlargement caused by the parasite, which is confined to the soft, parenchymatous tissue surrounding this woody strand. There is, therefore, little or no interference with the ascending stream of water.

The occasional formation of tumours near the surface of turnips which already show considerable secondary thickening suggests that the parasite can enter the root long after the root-hairs have been shed.

#### REACTION OF THE SOIL

Three pots were filled with infected soil of practically neutral reaction; to one 5 per cent. of calcium carbonate was added (to keep it neutral), to another sodium carbonate, and to the third sulphuric acid. The two last pots rapidly lost their pronounced reaction, and the dressing had to be repeated frequently throughout the season. Of sodium carbonate, 0.2 per cent. was mixed with the surface soil at sowing, and smaller amounts were added throughout the season as tests indicated the alkalinity was falling. The reaction of the sulphuric acid pot was maintained by watering twice weekly with a 0.1 per cent. solution. Turnips were sown, and by the end of the summer the results were as shown in Table I.

Table I

	Total plants	Number diseased
Sodium carbonate	18	0
Calcium carbonate	13	4
Sulphuric acid	12	12

In all experiments on soil reaction, the tumours were examined microscopically to make certain that they were caused by *Plasmodiophora*. Within five weeks of sowing a duplicate experiment was started with an additional pot, kept acid with phosphoric acid. This experiment (Table II) was also conducted with turnips, and the reactions were maintained as before.

Table II

	Total plants	Number diseased
Sodium carbonate	7	1
Calcium carbonate	7	3
Sulphuric acid	7	7
Phosphoric acid	7	7

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Owing to my absence towards the end of the experiment, the dressings were not continued until the end of the growing season; this probably explains the occurrence of some disease in the sodium carbonate pot, as, when the last dressings were applied, none of the plants in this pot appeared diseased.

The following duplicate experiment, also with turnips and in pots, was conducted the next season:

Table III

	Total plants	Number diseased	Total plants	Number diseased
Control—no dressing	8	4	8	3
Sulphuric acid	10	10	* <sub>0</sub>	* <sub>0</sub>
Phosphoric acid	10	7	6	5
Acetic acid	10	9	Omitted	Omitted
Quicklime	10	0	5	0
Caustic potash	10	0	6	0
Sodium carbonate	10	0	6	0

\* Killed by strong acid in mistake.

In these experiments the reactions were maintained by watering thrice weekly with 0.3 per cent. solutions (saturated in the case of limewater) of the respective dressing. It will be noticed that acetic acid has the same encouraging effect as sulphuric and phosphoric acids, and that caustic potash and quicklime check the disease as effectively as sodium carbonate. We may therefore conclude that acidity is favourable and alkalinity unfavourable to the development of *Plasmodiophora*.

These experiments confirm those of Massee (1895) and Halsted (1896). They also explain the encouraging effects of dissolved manures containing an excess of acid; and the preventive action of wood ashes (Berkeley, 1856; le H., 1879). In Switzerland, in recent years, sodium carbonate has been recommended for application to infected soil to prevent finger-and-toe (Osterwalder, 1929), whilst in the United States, Chupp (1928), has shown that the disease increases very rapidly with increasing soil acidity.

In the following experiment, carried out with turnips in pots, the dressings, at the rate per acre stated, were mixed with the surface soil in spring just before sowing.

Table IV

Dressing	Total plants	Number diseased
Quicklime (2½ tons) " (5 tons)	7	5
Calcium carbonate (2½ tons) " (5 tons)	8	1
Calcium sulphate (1 ton) " (2 tons)	8	5
Potassium sulphate (½ ton) " (1 ton)	7	7
Untreated	7	6

As regards the action of quicklime, the number of diseased plants suggests that two and a half tons had done no good, whereas five tons almost entirely prevented the disease. There is, however, another important fact to record, namely, that until early in August the plants in both quicklime pots were all healthy, whereas at this date all the other pots, particularly the four receiving sulphates, had several diseased plants. Later in the season, the majority of the plants in the pot receiving quicklime at the two and a half ton's rate were attacked.

The following experiment, conducted with mustard, shows that the disease can be entirely prevented by quicklime, provided sufficiently large dressings are applied to the growing crop and frequently repeated.

Table V

Quicklime applied (rate per acre)	Total plants	Number diseased
Pot 1. Control (no dressing)	25	18
2. 5 cwt. repeated six times	20	6
3. 10 „, repeated six times	24	2
4. 20 „, repeated six times	23	0
5. 20 „, repeated thrice	15	0
6. 40 „, repeated thrice	33	0

The dressings in pots 2, 3 and 4 were applied and mixed with the surface soil on May 9th (immediately before sowing), June 1st and 14th, July 1st and 14th, and August 1st; and in pots 5 and 6 on May 9th, June 14th and July 14th. As will be seen from the table, they all materially reduced the disease, though only the last three dressings were sufficient to prevent it entirely.

By means of alkaline dressings, therefore, it is possible to delay infection, and if the alkalinity be maintained by repeating the dressings, the disease can be prevented. The frequent though delayed infection appearing in these experiments in pots dressed with quicklime allows one to infer that this substance, when applied to farm crops during or just before the growing season, acts in this way. It does not kill the fungus but merely keeps it in check, and as soon as the alkalinity falls the fungus again becomes active. Bremer (1924) also found that lime does not kill the spores.

In these experiments it was noticed that the degree of alkalinity required to hold *Plasmodiophora* in check was not detrimental to the host—indeed, the plants seemed to thrive better in slight alkalinity.

Acids encourage the disease; under acid conditions, plants are attacked early and turnips usually die off. Alkaline dressings, even when not repeated, delay the date of attack, and there is much less injury to the host. Thus, in one experiment (Table I), the turnips in the sulphuric acid pot, which were sown in May, were attacked very early and were all dead by the first week in August; whilst of the ten

plants, all diseased, in the pot dressed with the same acid (Table III), only two were alive at the end of the season. The delay in infection due to sodium carbonate (Table II) and to quicklime (Table IV) has already been referred to. There is thus a relation between the reaction of the dressing, the date of attack, and the amount of direct injury suffered by the host.

Under the influence of alkaline dressings infection is at least delayed, and the plants, even if diseased, are usually alive at the end of the season, whereas with acid dressings many of them die off early. Hence, in comparing the effect of preventive dressings, figures based on the number of diseased plants at the end of the season are apt to be misleading. Jamieson (1881) and Middleton (1902) have called attention to this in connection with field experiments.

#### CAN THE DISEASE OCCUR IN SOILS RICH IN CALCIUM?

That soils deficient in calcium are very subject to the disease has been well established by numerous soil analyses (Johnston, 1849; Voelcker, A., 1859; Voelcker, J. A., 1894; Gilchrist, 1896; etc.). To test whether richness in calcium confers immunity, a series of pot experiments with mixtures rich in calcium, and a series of analyses of soils expected to be rich in lime, were performed.

The pots were in duplicate and those of Series 1 (Table VI) were filled with mixtures of chalk and soil, the percentages stated being dry (moisture-free) chalk and dry soil. The chalk used was from the Chalk Formation, and analysis showed it to be practically pure calcium carbonate. Turnips grown the previous season were used for infective material and turnips were sown. Series 2 was prepared in exactly the same way, except that horse dung (litter-free) was mixed with the soil in each pot.

Table VI

	Series 1		Series 2 (Horse dung added to each pot)	
	Total plants	Number diseased	Total plants	Number diseased
100 % chalk	8	0	7	5
70 % chalk + soil	7	0	7	4
30 % "	8	0	7	7
10 % "	11	2	7	6
5 % "	7	5	8	7
2 % "	8	5	8	8

The table shows that the disease can occur in a highly calcareous soil and confirms the experiments of Potter (1896). The only pots in which the disease did not appear were three of Series 1, but in the light of subsequent experiments, the dryness of the soil here was

sufficient to account for the absence of disease. The object of adding horse dung in Series 2, and its effects, are discussed on p. 122.

### SOIL ANALYSES

Each of the two gardens attached to the Agricultural Department of Armstrong College had a series of ten plots which, in 1895, were infected with diseased soil and had since been under experiment for the eradication of the disease. The two sets were duplicates, and a full account of their treatment and the results are given by Somerville (1894, 1895). These plots were selected for analysis because they were carrying affected crops and yet, as far as could be judged by rough tests, were rich in lime.

The soil of each plot was sampled in three places to a depth of one foot, and all estimations were made in duplicate. The results are given in Table VII. "Stones" refers to the portion which would not pass through a sieve with four meshes per linear inch, "Fine Soil" being what did pass through. The percentages of stones are given to make it possible to compare the figures with results which are expressed on the whole soil. The soil, as distinguished from the sub-soil, was about one foot deep, and the physical character varied considerably.

Table VII

Plot	Treatment	Percentage of stones	Percentage of total calcium in fine soil, calculated as		Percentage of available calcium in fine soil, calculated as $\text{CaCO}_3$
			CaO	$\text{CaCO}_3$	
Applied in 1896					
1	1 ton lime	7.93 (7.28)*	2.38 (1.40)*	4.25 (2.50)*	1.71 (0.48)*
2	2½ tons lime	6.03 (6.10)	2.13 (1.77)	3.80 (3.16)	1.55 (0.92)
3	5 tons lime	5.68 (7.05)	1.97 (1.76)	3.51 (3.14)	2.03 (1.29)
4	Bleaching powder	5.76 (7.25)	3.02 (1.75)	5.39 (3.12)	1.35 (2.18)
5	Copper sulphate	9.16 (5.10)	1.79 (1.58)	3.19 (2.82)	0.74 (0.61)
Applied in 1898					
6	Untreated	8.94 (7.27)	1.75 (2.59)	3.12 (4.62)	0.87 (2.39)
7	1 ton lime	6.42 (11.01)	2.19 (1.57)	3.91 (2.80)	1.50 (0.95)
8	2½ tons lime	8.75 (7.93)	2.13 (2.69)	3.80 (4.80)	1.35 (2.40)
9	5 tons lime	7.25 (7.85)	3.65 (1.53)	6.51 (2.73)	3.67 (1.09)
10	Copper sulphate	5.51 (7.11)	2.04 (1.42)	3.64 (2.53)	1.42 (0.61)

\* The figures within brackets refer to the South Garden; the others to the North Garden.

The analyses show that the soil of the plots is very rich in calcium. Thus, calculating as carbonate, the lowest percentage is 2½, four plots contain between this and 3 per cent., ten between 3 and 4 per cent., and five above 4 per cent.; one contains even as much as 6½ per cent. A high calcium content need not, therefore, be a safeguard against the disease.

The amount of calcium present in an available form was also estimated. This was done by determining volumetrically the carbon dioxide expelled by dilute hydrochloric acid and calculating it to its equivalent of the carbonate. Even with calcium carbonate as thus determined the plots are all abundantly provided; the lowest contains nearly  $\frac{1}{2}$  per cent., six contain between this and 1 per cent., eight between 1 and 2 per cent., four between 2 and 3 per cent., and one even contains over  $3\frac{1}{2}$  per cent. Richness of a soil, even in calcium carbonate, therefore, does not necessarily confer immunity.

That the disease can occur in highly calcareous soil, and yet that soils naturally rich in calcium are much less subject to the disease than those deficient in it, must both, therefore, be accepted as established.

It has already been shown that lime can prevent the disease by making the soil alkaline, but it could do this only if applied to the growing crop or shortly before sowing.

But lime can also prevent the disease in another way, for which it needs time—often several years. The precise nature of its preventive action here is not yet known, but the cumulative evidence of farm practice and of numerous field experiments leaves no doubt as to the fact of its efficacy (Gilchrist, 1905). From the slow nature of its action it may reasonably be concluded that it is very indirect.

#### ACTION OF NEUTRAL SALTS

To test the action of neutral salts on the disease, the neutral phosphates, sulphates and nitrates of potassium, sodium and calcium, were applied to pots of infected soil. The experiment was carried out in duplicate. In the mustard series (Table VIII), the dressings, at the rate of a ton per acre, were mixed with the soil at potting time, while in the candytuft series they were applied in water (0.2 per cent.) twice weekly.

Table VIII

	Mustard		Candytuft	
	Total plants	Percentage diseased	Total plants	Percentage diseased
Control (no dressing)	40	39	47	30
Neutral potassium phosphate	47	43	60	36
Potassium sulphate	46	39	50	50
Potassium nitrate	39	8	70	14
Neutral sodium phosphate	33	33	47	27
Sodium sulphate	36	29	54	44
Sodium nitrate	45	7	53	19
Dicalcic phosphate	40	55	79	26
Calcium sulphate	35	30	72	30
Calcium nitrate	35	11	65	12

All three nitrates, in both series, markedly reduced the disease. In the mustard series they gave an average of under 9 per cent.

diseased, whereas the control pot contained 39 per cent., and the other six from 29 to 55 per cent. In the candytuft series the nitrate pots averaged 15 per cent. against 30 per cent. in the control, and from 26 to 50 per cent. in the others. This experiment was repeated the following season, again in pots and in duplicate, the soil being sandy with some humus. The results were very similar except that there was less disease in the undressed pots.

In the experiment shown in Table IV sulphates of both calcium and potassium caused the disease to appear earlier than in any of the other pots, and the attacked plants in the sulphate pot were visibly dying of the disease early in the season. The earlier appearance of disease is evidence that sulphates encourage the fungus, but the total number of turnips grown in the pots is too small to admit of accurate comparisons based on numbers. The soil was rich in organic matter.

The encouraging effects of sulphates were not noticed in the experiment with mustard and candytuft described in Table VIII. Earlier infection is not excluded, however, as mustard and candytuft show no symptoms of infection apart from the tumours which are usually hidden in the ground, whereas in turnips early infection is evident from the wilting of the leaves.

Thus in one experiment nitrates reduced the disease and in another sulphates encouraged it, but the principle underlying the action of neutral salts is not apparent from these experiments.

#### AN EFFECT OF ORGANIC MATTER

Some years previous to this work, Prof. Potter observed that a piece of ground to which he had applied a watery extract of horse dung produced the disease much more virulently than it had ever done before. This observation was followed up by several experiments, in which the pots were of burnt clay, the horse dung was the solid excreta, free from litter, and the sand pure washed silver sand, containing less than 0.1 per cent. available organic matter. Where sand was used without dung, a small amount of mineral matter was added to supply the elements essential for growth. Crushed turnip tumours were used for inoculation.

In two pots, one of silver sand and the other of the same material mixed with horse dung, both artificially infected, turnips were grown, with the following result:

	Total plants	Number diseased
Pure sand, plus essential minerals	20	0
Pure sand, plus horse dung	12	10

The results suggest that organic matter is essential for the occurrence of the disease, and this seems to be confirmed by the Chalk

Experiment (Table VI, p. 119), which was carried out the same season. The chief object of this experiment was to ascertain whether it is possible for the disease to occur in a highly calcareous soil, but a duplicate series of pots was added, in each of which a heavy dressing of horse dung was mixed with the soil. In pots containing 30 per cent. or more of chalk the disease occurred only where horse dung was added; and in those containing less than 30 per cent. chalk the addition of horse dung increased the amount of disease.

Tests of the reaction of the pots of the Chalk Experiment throughout the season showed that the horse dung increased the alkalinity, so that the dung was evidently not favouring the disease by making the soil acid.

Potter's observation was based on the use of a watery extract of dung, and the only other likely explanation of its action is that organic matter is needed as food for the fungus—in other words, that *Plasmodiophora* requires to lead a saprophytic existence in the soil before entering its host. This would be extremely important, and it was therefore decided to repeat the sand experiment.

The experiment was performed in duplicate with mustard and candytuft, with the following result:

	Mustard		Candytuft	
	Total plants	Number diseased	Total plants	Number diseased
Pure sand with essential mineral (inoculated)	30	19	51	11
Pure sand and horse dung (inoculated)	40	24	135	50
Sand and horse dung (control—not inoculated)	60	0	—	—

The experiment showed that the disease could occur in the absence of organic matter.

The problem now was to reconcile this result with that of the previous season. Apparently the chief difference which could be of importance between the two sets of sand pots lay in the amount of water given. Those of the first year had been watered only once a day, whereas in the following season they had been watered twice daily. As a consequence, the pure sand pot in the former was often dry, while in the latter the sand remained comparatively moist. On this interpretation the disease should occur in soils devoid of organic matter provided the soil be kept sufficiently moist. This was tested in various ways. In one experiment two pots of the same sand as in the last experiment were taken. Pot A was kept continuously wet throughout by standing it in a bowl of water which was never allowed to go dry, while pot B was kept comparatively dry by giving it free drainage and watering only once daily. At the end of the season pot A had seventeen plants, of which nine were diseased, and

pot B ten plants, all unaffected. In a duplicate, conducted in the same sand, pot A had seven diseased plants out of a total of thirty, but pot B was kept so dry that the plants died prematurely.

Another medium devoid of organic matter in which the disease occurred, provided it was kept moist, was one consisting of the same kind of sand mixed with kaolin.

On the other hand, it was shown that the disease could be prevented in a soil rich in organic matter by keeping the soil dry. Thus, in a mixture of sand and horse dung (which was known from other experiments to be suitable to the disease) with which this precaution was taken, only two plants out of thirty were diseased; and in a duplicate pot, containing fourteen plants, all remained healthy.

The retention of moisture, then, was the explanation of the influence of horse dung in my experiments, though this interpretation is not applicable to the case observed by Potter.

The disease has been recorded in water cultures, in which there would presumably be no appreciable amount of organic matter.

In the initial stages of these experiments on organic matter, well-burnt ashes were employed in one experiment as a medium of growth. Analysis showed them to be suitable for this purpose as far as the available organic matter was concerned, but no disease occurred either in the ashes alone or in the pot containing ashes mixed with horse dung. In the light of other experiments then in progress, the pronounced alkalinity of the ashes was a sufficient explanation of the absence of disease.

#### GERMINATION OF THE SPORES

Periodically during two years attempts were made to induce the spores to germinate. The attempts were made at all seasons, in a great variety of substances and generally under very diverse conditions, but always with negative results. Meyer (1888) and Frank (1896, 1897) record a similar experience, though Woronin (1878), Rostrup (1885) and Chupp (1917) report having observed the germination.

In two successive seasons, towards the end of May, the majority of the spores in some diseased roots produced the previous year and lying in a heap out of doors were found to shrivel and die. There was no evidence that they had germinated, and attempts to observe the germination of the few unaltered spores also failed. Meyer (1888) records a similar experience.

ARE THE SPORES CAPABLE OF IMMEDIATELY  
INFECTING ANOTHER PLANT?

In July, diseased turnip tumours grown that season were washed to remove anything that might be adhering to their surface and used to infect pots, the soil in which was free from disease but known from other experiments to develop the disease after infection. The pots were sown on July 20th with turnips, candytuft and mustard. On October 15th, when the plants were harvested, they were all free from disease. The results suggest that the spores are not able to infect another host in the same season.

Soil at Halle that had borne badly diseased plants that season was sown with mustard on November 14th. When the plants were taken up on March 15th following, none were diseased. This suggests that infection does not occur during winter.

TO WHAT DEPTH IN SOIL CAN THE SPORES INFECT PLANTS?

Infective material was sown on the floor of trenches two, four, six, eight, ten and twelve inches deep, care being taken that none came in contact with the sides of the trenches, and these were afterwards filled up level and sown with turnips. Plants were attacked in all the trenches, but it was found that in the deeper trenches the tumours were confined to the approximate depth at which the spores were sown. This was particularly noticeable in the twelve-inch trench, and suggests that the parasite settles in the host near its point of entrance.

The soil was light and porous in character, and for some years previously had been cropped with lucerne, the roots of which no doubt kept it open. This experiment was on the same lines as that of Potter (1896), where in strong clay the disease occurred to a depth of only six inches.

GENERAL SUMMARY

1. Attempts to infect with *Plasmodiophora*, plants allied to Cruciferae taxonomically, or with a similar ash composition, gave negative results.

2. The injury done by *Plasmodiophora* to its host depends on the species of the host and on the age at infection. Some species are apparently uninjured. Where considerable direct injury was suffered the continuity of the vessels was found to be broken.

3. Acidity is favourable and alkalinity unfavourable to the development of the disease. By means of alkaline dressings infection can be delayed or entirely prevented. Quicklime when applied to the

growing crop inhibits the disease by its alkalisng action. Lime can also prevent the disease in some other, as yet unknown, manner, for which it needs considerable time.

4. The disease can occur in highly calcareous soils and yet soils naturally rich in calcium are much less subject to the disease than those deficient in it.

5. The application of sulphate to soil encourages the fungus as judged by the earlier appearance of the disease.

6. A moist soil is favourable to the development of the disease.

7. The presence of organic matter in soil is not necessary for the development of finger-and-toe, though it may encourage the disease by enabling the soil to retain its moisture.

8. Attempts to observe the germination of the spores failed. Experiments suggest that the spores are not able to infect another host in the same season and that infection does not occur during winter.

9. The spores were found to infect plants to a depth of twelve inches in soil.

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## L. G. WINDT AND HETEROECISM

BY J. RAMSBOTTOM

THE history of the discovery of heteroecism is of considerable interest. There are several accounts of the early belief that the presence of barberry is harmful to corn but few of them refer to L. G. Windt's *Der Berberitzstrauch, ein Feind des Wintergetreides*, published in 1806; indeed the only mention in readily accessible works is in Klebahn's *Die wirtswechselnden Rostpilze*, pp. 210-13 (1904). Windt's book is apparently very rare, for the only copy I can trace in this country is in the British Museum. However, in the Department of Botany there is a manuscript translation which was formerly in the possession of Sir Joseph Banks. It was written in Banks's library but I cannot recognise the handwriting\*. The title is given as "The Barberry-bush an enemy to winter corn, proved by observations, experiments and testimonies by L. G. Windt, counsellour in the chamber of accounts of the Count De Lippe Schaumberg."

It is not an easy matter to assign the proper amount of credit due to individuals for the part they played in the controversies that took place on the subject of heteroecism at the beginning of last century. Too much stress is likely to be given to those points which in later days were proved, with the omission of others which were wide of the mark. Bearing this in mind, however, I feel that Windt has not received his due share of the credit. This may have been because of the scarcity of his book, but no doubt its haphazard arrangement counted against the acceptance of the evidence brought forward; it might almost be said that the only orderly part of the book is the preface. "The honoured reader will easily perceive that the observations and transactions, which I here lay before him, were not, with the exception of a few extracts from newspapers and journals, originally intended for the press.

"In the year 1804, I was led into an examination... whether Barberry bushes were hurtfull to wheat and rye, growing in their neighbourhood. I had probable grounds of suspicion, and carried on my inquiries with all the attention that other avocations and duties would permit, though solely with a view to the benefit of my prince and the advantage of that part of my fellow subjects employed in agriculture. But when the hurtfullness of the Barberry appeared to be fully verified,

\* "Not carrying with me the German text to Sir Joseph's library I had added the erased most important paragraph." MSS. p. 102.

Errors in the spelling of names of both fungi and botanists have been corrected in the extracts quoted.

I felt myself compelled by duty to make a communication of this fact to the *Imperial Intelligencer*\* and other public prints, that, after benefitting by the notices and advice of learned and experienced husbandmen, I might bring the matter, more confidently, before the Publick. I knew not, as yet, the bad reputation of the Barberry in Holland, England, and even in America. My acquaintance with books on rural economy was so scanty, that I had not heard of any discussions, or even hints, on this subject, particularly of what is said on it, by Mr Marshall, and Mr Begtrup....

“From the collections before me, the evil report of the Barberry will, I am convinced, appear to be by no means founded on vulgar prejudice: its destructive effects, talked of in many places, and still called in question, will be shown clearly to exist, and especially in the case of rye....

“Various occupations do not allow me to bestow more time on this work, than is necessary to explain, in an introduction, the disease in corn called rust, and to give some account of the Barberry, to whose operation this malady is ascribed: the remainder consists intirely of diaries, records, and testimonies; which documents I have obtained permission to publish, in consideration of their usefullness to the farmer. Had I been possessed of leisure and ability to reduce the materials of this work into a more regular composition, the Public would not probably be a gainer, since many internal marks of truth might thereby have been smoothed away, and effaced. Here, the whole rests on facts, which each reader will weigh for himself, without being anticipated in his judgement.”

It is interesting to note the circularising of the Press which was practically contemporaneous with the effort made by A. Young, the Secretary to the Board of Agriculture in this country, to obtain information from farmers, landowners and others about the cause of mildew in wheat and the effect of barberry (*Annals of Agriculture*, XLIII (1805), 457).

Windt began with very mixed ideas about the nature of the disease in corn and the manner in which barberry was connected with it. He sums up by saying “it would ill become me to perplex the learned reader by stringing one hypothesis on another, in order to defend my own conjectures. The operation of the Barberry may be referred to the article of occult qualities: it is enough for the husbandman to know that it hurts his corn.”

The diary and other documents “either wholly, or in abstracts” are given “according to the order of time in which they were collected.”

The first memoir is dated July 8th, 1804. It records that the great garden at Hockersau was, above eight years ago, hedged with Bar-

\* *Der Reichsanzeiger.*

berry, and that whenever sown with rye has suffered by mildew, and full details are given about neighbouring fields. The evidence is for the most part very clear: thus "the swathes, next to the hedge, looked like chopped straw: those farther off were less broken: but even in the divisions considerably remote, the rye was observed to look red or yellow." Windt's belief, however, was that barberry had a certain mischievous effect on wheat and at first he does not distinguish between rust and smut. Also he records without comment that "An enclosure had been made with this plant [barberry] round a field of Beans: the beans were ruined by mildew: the hedge was removed; and the evil ceased."

The memoir concludes: "When all these facts are considered, the mischievousness of this plant is rendered highly probable: yet the evidence falls short of certainty. Before condemning the Barberry to be rooted out, exact experiments should be made, so that every degree of doubt may be removed. This preliminary information I have laid before the Count's chamber, humbly wishing to be instructed whether the Barberry hedge should at all events be rooted out next harvest, and a different kind of hedge planted. If suspicions are confirmed by future experiments, it will be necessary for the benifit of agriculture, to root out the Barberry."

The memoir was not presented until August, by which time he had collected further evidence. He had become "so thoroughly convinced of the hurtfullness of the Barberry" that he proposed replacing it by hornbeam in certain named gardens. He submits certain proposals and says: "I thought it time, however, to render this account to the chamber, that, before the rye of this year is cut down, the facts, which I have stated, may be examined and verified by others at any rate, I think it should be ordered that private persons root out all Barberries from their grounds, under pain of punishment." In the appended notes he first describes an experiment of placing three boxes of rye plants, one on the north side of a barberry hedge almost touching the leaves, a second one hundred paces away and the third on the south side at an intermediate distance. The rye became infected, that on the south side less than the others. "I wished now to examine the field from which the boxes of rye had been taken; but the time for this had gone by." Observations were practically continuous—the account of the experiment is dated "morning of the 16th July 1804," the next observation "of the same date in the afternoon" and the following one "the same date—in the evening."

On August 18th he states that the rye in the field from which the boxes were taken "was mildewed, in the present as in the last year: the ears shrivelled or empty: a circumstance which leaves the effect of the Barberry doubtful." Later he had "recourse to the only other mode, by which the hurtfullness of this plant could be proved."

Towards the end of October 1804 he caused "eight of the soundest Barberry bushes bearing fruit" to be transplanted. "Two of them were placed near the rye, 40 steps asunder. A third was planted by mistake among wheat. At the distance of 800 steps from these three, the five others were planted among rye, distant 50 steps, respectively, from each other. It was scarcely possible that an experiment made on so large a scale should not afford conviction. To me, who was convinced already, it seemed grievous to destroy much good grain, but the present loss, I hoped, would be over balanced by future advantage."

This experiment was reported on as follows: "Agreeably to my received instructions, I planted a few Barberry bushes amidst the rye, in order to ascertain the effect: but did not discover, though frequent and curious in my visits, that the rye near to these decried bushes looked worse than any other. It seemed beautifull, even on the 27th of last month: but eight days later, that is, the 4th of the present month, I found, on examination, that it had begun to suffer from the dangerous neighbourhood. The evil has recently so much encreased, that the rye is now quite ruined, as the chamber will be concerned by the accompanying samples. This effect is the more striking, because the corn a little inward continues perfectly sound.

Maschvorwerk 8th July 1805  
Stahlhuth."

Windt proceeds: "The chamber of accounts and revenue does not in the least distrust the report of the able and respectable superintendent Stahlhuth, yet wishes to have it confirmed in a formal and legal manner. For this reason, the Baillif of Buckeburg is commissioned to take the evidence of intelligent farmers on the subject, who are to answer the following questions. I. How is it with the rye, as to the stem, leaves, and ear, in places contiguous to Barberries, compared with others more remote from them. Are there signs of disease? II. How is it with the Barberries themselves. Are they green and luxuriant, or decayed and weakly, with signs of malady on their leaves and branches? III. What is the state of the rye near to these bushes? Are the stalks and blades spotted? Are the ears well filled, or empty? Is the colour sickly? and what is the name of the malady with which they are attacked? IV. How many feet inward in the field, does the mischief extend? Is it always worse, the nearer you come to the Barberry. V. In other parts of the land, are there any signs of a similar malady?

"This commission was carefully fulfilled by the Bailif of Buckeburg."

Four farmers examined the field and their evidence is given. Summarising this: The rye was affected to from ten to fifteen paces round the bushes, and not elsewhere. The leaves of the Barberry bore "small

tubercles" in "dry spots." Two of the witnesses stated that rye was always diseased where barberry grew, that the disease was more severe near the barberry and chiefly in the direction of the wind. Windt himself visited the field on July 20th and found that by then the rust had extended to two hundred paces. So early as July 20th, 1804, Windt writes: "The thing, that I learned today, of most importance to my enquiry, was the following. I walked along the hedge enclosing H.—'s field, between the hedge and the rye. The shepherd's son had said, that here no barberries were to be found. I therefore passed forward, careless of the hedge, and looking only at the corn. At once I saw before me, rye in as bad a condition as at Hockersau close to the Barberry hedge; white, dry, the ears shrivelled, and the stems broken. It lay in a half circle of six paces in semi-diameter, from the main stock of the hedge. It seemed, as if it had been beat down with a club. This appearance, which very much surprised me, turned my attention to the hedge, where I immediately discovered a Barberry bush to be the source of the evil. I advanced straight forward amid the corn, and found, even where the stems were upright, the ears quite shrivelled; and the mischief extending deeply into the field. This striking observation, concurred with what is before said of H.—'s field, where the mildew in the rye increased with its vicinity to the Barberry, to assure me that this plant, at least in our climate, has the most pernicious effects. As far as the conviction of my own mind is concerned, I have no more inquiries to make." He, however, goes on accumulating evidence: "After such unequivocal proofs of the hurtfullness of the Barberry, two questions naturally arise, over what extent of country does its operation prevail; and secondly, does the Barberry, unaccompanied by circumstances, produce the mischief; or must not its hurtfull operation be aided by a certain disposition of the lower atmosphere." Regarding the distance these distinctive effects extend he says: "all my enquiries and observations show that these effects are striking and desolating in the distance of 10 or 12 paces. I have also perceived them visibly at the distance of 50, 100, 150 paces;" and a final attack "above 1000 paces."

"In the near neighbourhood of the Barberry, the rye is attacked before, or during the bloom: the rye farther off, I observed to be damaged later, yet totally; that still more distant, as the Horst field, yet later, and in a smaller degree, so that some produce might be expected from it: the remote fields Petzerhofe and Gevallernfelde, were injured the latest of all; from these observations, I conclude that the infection diffuses itself on all sides as from a center, and thus the extent of the mischief is very great."

Then follows the evidence of four farmers one of whom says: "In Eisbergen, the Barberry is called the air-bush, from a notion that it attracts the air. This plant grows in two places of a hedge there; the

rye is always rusty near those places, as may be seen remarkably in the present year."

The evidence up to July 20th was transmitted by Windt "to those concerned, and by them sent for the examination and opinion of a skillfull Botanist. This opinion was, that though the mischief from the Barberry seemed highly probable, yet, before the extirpation of so usefull a plant, more observations ought to be made, more experiments to be tried, and information obtained from different places, whether in them also, the Barberry was found to be hurtfull. Accordingly, I received instructions in the beginning of October. I. To root out the hedge 1,500 feet long round the great garden at Hockersau, and to plant another in its stead. II. To continue my observations and experiments. III. To make inquiry through the public prints, whether the mischievousness of the Barberry was elsewhere experienced."

Windt then sought information from a farmer who had Barberries in a hedge "contiguous to the tilled land of peasants there. The peasants imagined that their crops were hurt by the hedge, and entreated him to remove it. He hesitated, and endeavoured to reason the peasants out of their opinion. These continued to murmur, untill a compromise was entered into, by which the Barberries were removed, and a thorn hedge, at the expense of the complainants, planted in its stead. When this was done, the corn continued to suffer by mildew, as much as formerly."

The farmer answered all his questions, holding that "the whole parish saw that the expence of removing the hedge was thrown away." Windt's only comment is: "Mr Meyer reasons like an observing intelligent farmer. As the mildew happened, notwithstanding that the Barberries were removed, he could not regard them as its cause."

He reported to the chamber of revenue that he had "rooted out the hedge round the great garden of Hockersau (which was done in the first days of the month) and filled, with the useless bushes, a pond in the neighbouring meadow." To this I added, "That there were many Barberries mixed with other shrubs in the Bosquet of Klus, contiguous to the fields of Hockersau. I had not yet ascertained how far the mischief from Barberries extended; but had reason to suspect that it spread very widely, in consequence of the contagion diffused from one corn field to another. In the neighbourhood of such fields, I thought that Barberries ought not to be tolerated even in woods and thickets, because the infection from them might be conveyed by the air, and because they might, through inattention, be transplanted, and again employed as hedges. It appeared therefore highly proper, that they should be extirpated not only from the above mentioned Bosquet, but from the possessions of the peasants and others in the district of Hockersau and the adjacent villages. If this should be followed by

happy effects on the quality and quantity of the grain, the very extensive mischief from the Barberries would be clearly established. The Count's chamber, duly attentive to the interests of agriculture, determined, accordingly, that this opinion should be made known, and strongly impressed by the magistrates: that I should proceed with all diligence in my observations and inquiries; and, if these afforded the result expected by me, that the Barberries, a plant that might be well dispersed with, should be extirpated through out the whole country. According to these instructions, my conduct was regulated. The peasants, under the direction of a forester, laboured with alacrity in clearing the Bosquet of Klus the 18th of March: and in employing the rooted out bushes, which had been piled up in an open field, to fill pits in the neighbouring meadow. In other parts of the country, the magistrates were contented to injoin, but the Baillif of Buckeburg commanded the extirpation under pain of punishment. A few years will determine, whether the mildew may be prevented, that has impoverished so many substantial farmers, and which beggared many in 1805."

The next observation deals with a disease of sheep thought to be in some way associated with rust and "Barberries at least cooperate."

He next mentions a field with two barberry bushes in each of two hedges: the rye was then healthy, but he asks that the field should be examined later and forecasts what would be seen. They were examined on May 25th and found to be free of rust. The same two observers again visited the field on July 25th and reported that where the barberry bushes grew the rye was rusted, the disease decreasing with the distance from the bushes. In another field no barberries grew "and here the rye was in the soundest and most healthy state possible."

On August 1st he examined some fields and found the corn in one totally ruined though more distant from the barberry and separated from it by two hedges by a causeway with trees on either side and by a deep stone quarry. "The difference, I think, arises from the wind, which, for a month past, has blown chiefly from the west, changing to the east seldom, and that only for a moment. The west wind conveyed the pernicious influence of the Barberries to the Black close: but the fields west of the Bosquet, naturally escaped the contagion. This observation seems conclusive; though the only one of the kind that it has been in my power to make. If the mischief done by the Barberries depends on the state of the wind, it is clear that their operation consists, not as many country-people imagine, in drawing the healthfull influence from the air, but, on the contrary, in exhaling something that is pernicious, whose effects appear in those fields to which the wind carries it."

He adds a note regarding the possibility of other plants being de-

leterious to corn and records that a twig of *Cornus sanguinea* was brought to him from a field which, although without barberries, had rye completely ruined by rust. The *Cornus* had diseased leaves "as the leaves of plum-trees are, when attacked with what is called the honey-dew."

He ends his own observations thus: "My remarks are now concluded, and I have only to mention what was done in consequence of them.

"When the Barberry bushes among the rye were removed, and the corn brought from the fields, I considered the business as ended. The hurtfullness of these bushes was now evinced by my own observations and experiments, by the communications and testimonies of others. The chamber of accounts, taking all this into serious consideration, declared that the question was decided as clearly as the nature of the thing admitted, or as practical purposes required. Accordingly, the matter was laid before government, and a general order issued. I. That all Barberry bushes should be rooted out from hedges, gardens, fields, or plantations near fields, before the 1st December 1805. II. That persons contravening this order should be fined two dollars. III. That the fines should be bestowed in rewards to informers. By these means, the Barberry has been extirpated from the district of Buckeburg, where it formerly abounded; or, if any lurks concealed here or in other parts of the country, it will certainly not be able to defend itself against the zeal and avidity of informers."

For the convenience of his readers he adds the principal articles that have appeared on the subject in the newspapers during the past year: others he summarises. As is to be expected, the correspondence is not one sided. Much additional evidence is given, however, of the effect of the barberry.

Although they do not concern Windt's own work it will not be out of place to consider the three most important articles.

The first is by Baron von Montelon. It is an account of the injury done to winter corn and imputed to the influence of barberries, a paper read before the Economical Society Brandenburgh, November 9th, 1804, and published in the *Imperial Intelligencer*, No. 26, January 28th, 1805. It gives a clear description of various observations from 1800 onwards. When describing the effect of some barberry bushes on rye he adds: "Comprehended between two sides of this lost rye, the north and east side, I had sown 30 bushels of wheat; this continued to be good. It yielded 338 shocks, from which were threshed 375 bushels\* of fine sound wheat. The rye plants that happened to grow amidst this wheat, were as bad as the rest; whereas the wheat stalks that grew among the diseased rye, remained perfectly sound. This circumstance seems the more worthy of notice, because the English writers on husbandry, and particularly Mr Marshall, complain of the

\* "He says 15 wispehn and 15 scheffel. A wispehn is 24 scheffel, or bushels."

mischief accruing from Barberries to wheat. The wheat here, was indeed 1,000 paces from the pestiferous bushes. Notwithstanding this distance, the rye was destroyed. A peasant sowed a single bushel of wheat, at a considerable distance from mine, but nigher the vineyard; this continued in the midst of the shrivelled rye."

Klebahn recognises this as an early record of specialisation.

Two other notes may be given in full.

The first is "Conjectures on the cause of the pernicious influence of the Barberry on rye occasioned by the communications in the Imperial Intelligencer, No. 36." "The Editor of those remarks wishing for the opinion of others concerning the cause of the pernicious influence of the Barberry, I venture to impart my thoughts on the subject, hoping for indulgence as I am neither a philosopher nor an agriculturist. I am perswaded that the black spots, like fly-bites on rye and barberry, are nothing else but small fungi or mushrooms. These grow on many other kinds of plants, witness different sorts of *Erysiphe*, *Aecidium*, *Puccinia*, *Uredo*, etc., and most commonly on the leaves. In my opinion the spots on Barberry are nothing but the *Erysiphe Berberis* (Hedw.) which usually grows on the leaves, and whose wonderfully small seeds, being carried towards corn fields by the wind, fix their roots and vegetate in the stems, depriving them of their juicy nutrient, and thereby rendering the ears small or empty. As these diminutive mushrooms attain puberty in a very short time, (which is the case with the *Mucor Mucedo* of Linn. and various other kinds) and the seeds are thus again shortly fit for the reproduction of new seeds, which are carried by the wind to neighbouring fields, it seems likely that one ear infects another, and when the wind continues constant for a considerable time, that the contagion may thus spread very widely. It would be of importance to examine by the microscope whether these small, spot-like, mushrooms on the Barberry, are of the same sort with those on rye. I greatly wish that some skillfull Botanist a Persoon, Bridel, Wildenow\*, Roth, or Sprengel, would communicate their remarks on this subject in the *Imperial Intelligencer*. That the flower dust, or vapour from the plant, should extend to such distances, does not appear very probable.

E—s—n berg. 14th Feb. 1805."

The second is "Natural Knowledge. Influence of the Barberry on Corn, in reference to No. 188 of the *Imperial Intelligencer*."

"Where experience pronounces clearly, all doubt ought to cease.

\* C. L. Wildenow (*Beitr. Naturh. Fr.* Weber und M. H. Mohl (1805), p. 132) from observation concluded that *Aecidium Berberidis* produced *Uredo linearis* on corn. He rubbed leaves of *Elymus*, *Populus balsamifera* and *Sorbus Aucuparia* with infected barberry leaves. He found a small area of rust on the poplar and stated that *Aecidium Berberidis*, *Uredo linearis* and *U. popularis* were forms of the same growth, the epidermis of the host plant determining the form of the parasite. The genera *Aecidium* and *Uredo*, therefore, should be sunk and he proposed the name *Ustilago pulvis* for the fungus to prevent confusion. He published no further account, though he had intended repeating his experiments the following spring.

That Barberries occasion rust and the failure of crops, is a conclusion forced on me by my frequent botanical excursions through this country. For this conclusion, I have now found the completest authority in a most interesting paper on the trust-worthy Sir Joseph Banks: 'A short account of the disease in corn, called by Farmers the Blight.' In the country near Rollesby in Norfolk, where Barberries abound, the wheat so seldom thrives that the place has acquired the name of mildew Rollesby.

"But the manner in which Barberries operate their mischievous effect, is not easily explained. The pollen or fecundating dust of their bloom is not calculated for such a purpose: this waxy substance is altogether harmless.

"It is known that Barberry-leaves are much infested with a fungus (*Gastromgius*) the *Aecidium Berberidis*, first delineated by Jacquin (*Collect. vol. 1, Tab. 4*) and afterwards by Rebentisch (*Flor. Neomarch. Tab. III, fig. 2*). The rust in corn is commonly called *Uredo*, and held to be merely a powder which corrodes and cracks the Epidermis. But the more accurate observations of Persoon (*Dispos. Math. fung. t. III, f. 3*) and of Banks (*l.c. Tab. 1*) prove it to be a *Puccinia*, called the *Puccinia graminis* by Persoon (*Synopsis fung. p. 228*). Magnificent, exquisite, incomparable are the delineations which Banks, with assistance of the King's botanical painter Francis Bauer\*, has given of this production in the work above cited. I lament that this small work is not on sale, and only given by the author in presents; for the art with which these microscopic bodies are represented is worthy of the greatest admiration.

"We here see clearly how these fungi insinuate and root themselves in every fissure of the stalk or leaf, how they project from a small tubercle, are formed into a pear-like body, divided by a septum, finally how they burst at the upper end, and scatter their seeds. Banks reckons that every fissure (and there are 500 fissures within the 12th part of a square inch) contains from 20 to 40 of these mushrooms. He shows that the countless multitude of these mushrooms robs the corn of its nourishment, and prevents the developement of its grains. All this is most excellently explained by him.

"The mushrooms on the Barberry, and those called rust on corn, belong to the same family (*Gastromgi*) but are not of one genus. The *Aecidium* has cylindric seed-bags, which burst with notched openings. The *Puccinia* has top-shaped seed-bags, separated by partition-walls or septa. Is it possible for one genus to change into another? Not surely, in completely organised plants. An oak cannot become a beech; nor a pear-tree, an apple-tree. But, here, are most diminutive productions whose whole vegetable character is stamped at once in their formation. May not the seeds of *Aecidium Berberidis*, by trans-

\* Francis Bauer's original coloured drawings of "Diseases in Corn" are in the Department of Botany, British Museum (Natural History).

plantation on grass or corn be converted into *Puccinia graminis*? I do not assert that this happens: I only ask the question.

“SPRENGEL, Professor of Botany.”

The book ends with a summary of Banks's well-known letter: “I did not choose to conclude and publish this work, until I had seen the account written by Sir Joseph Banks in 1804.” Windt gives a very full summary of it and makes microscopical examination which leads him to the discovery that the rust spores in rye were egg-shaped, whereas those in wheat were round—a morphological difference of some importance. “I readily renounced my former opinion: my own eyes now convinced me that what I had taken for mere globules of sap, consisted of finely organised bodies. The passages in which I had proposed my erroneous hypothesis, it is too late to cancel. My main object, however, is not affected by this error, and I am happy to have come at the truth, tho' by a circuitous route. I leave it to philosophers to explain why the rust scratched from stalks of rye, is egg-shaped, and that from wheat, spherical; and also to determine whether the same kind of mushrooms may not assume different forms when nourished by these two plants, through the difference in their sap.” Klebahn points out that it is probable that the wheat was infected with *Puccinia triticina* or *P. glumarum*, not with *P. graminis*.

Windt is not fully satisfied that the spores from the rust on barberry can “take root on corn in whatever condition it may be, diseased or sound....Is the blight in corn caused merely by the vegetation of small parasitic fungi, or must not a chemical ferment concur, communicating from one plant to another, chillness, corruption and a stopping of the circulating juice?”

“I conclude this book in the perswasion that, the point, which I aimed at, is established....To those still inclined to regard the Barberry as innocuous....I would only make the request, that these no longer urge their opinion on abstract and general grounds, until they have collected the result of impartial observation and carefull experiment. To be convinced by their own eyes let them plant Barberries among rye, and compare their effect with that of hazel or horn-beam: towards the end of June let them cut off a few Barberry-branches with their leaves, some of which branches are infected with rust, and others in a sound state. Let them be respectively scattered in different places among the corn, and the consequences carefully remarked. Justice requires, not only that such experiments should, by every man, be confined to his own possessions, but that, for the safety of his neighbours, the deleterious vegetables should be destroyed, as soon as their operation has been ascertained.” He aimed at the extirpation of the Barberry “so completely, that no mischievous vestige of it shall remain in our fields” so that in a few years in the northern parts of Germany it would be “as rare an object as the palm-tree of the East.”

A DISEASE OF POMEGRANATE (*PUNICA GRANATUM* LINN.) DUE TO *AMPHICHAETA PUNICAE* N.SP.

BY H. CHAUDHURI AND JAGTAR SINGH

(From the Department of Botany, Panjab University, Lahore)

(With Plate II)

THE disease was noticed on the nursery plants in Lawrence Garden, Lahore. The twigs of the infected plants bore innumerable minute fruit bodies of *Amphichaeta* (Pl. II, fig. 1). The disease was confined to the twigs. Infected plants were seldom killed, but they were much stunted in growth. Hand sections and microtome sections 8  $\mu$  thick were made. These showed hyphae mainly in the vessels of the secondary wood (Pl. II, fig. II), with some also in the cortex and in the pith.

The hyphae are branched, generally unseptate, and occasionally dark coloured. Acervuli are freely formed on the surface of the twigs as well as in culture. They are of various shapes and sizes and contain numerous conidiophores bearing conidia.

The fungus is placed in the genus *Amphichaeta* McAlp. for the following reasons. The spores are borne in acervuli (Pl. II, fig. VIII) with a stroma-like stratum without setae and are not borne in chains; they are dark, at least in part, and the conidia are uniciliate at each end. The spores are large, measuring 22–27  $\times$  7–11  $\mu$ , spindle-shaped, and 5-septate, the four middle cells dark coloured, the terminal cells hyaline. Both the cilia are sharply curved usually on the same side (Pl. II, fig. III). The conidia are borne singly at the tips of the branches of conidiophores (Pl. II, figs. VI, VII). Sometimes two or more conidia may be borne on a single conidiophore.

As this species differs materially from *A. Kennedyae* McAlp. and *A. Davisiae* McAlp., it is regarded as a new species, with the following description:

*Amphichaeta Punicae* n.sp. Acervuli black, erumpent, scattered, conidia somewhat spindle-shaped, 5-septate, measuring 20–27  $\times$  7–11  $\mu$ , the four inner cells dark coloured, the two terminal ones hyaline, each end cell bearing one-cilium. Apical and basal cilia similar, 6–10  $\mu$  long and both sharply curved, usually on the same side.\*

*Hab.* On twigs of young plants of *Punica granatum* L. at Lahore, India.

\* *Amphichaeta Punicae* sp.nov. Acervulis nigris erumpentibus, sparsis; conidiis aliquantum fusiformibus, 5-septatis, 20–27  $\mu$  longis, 7–11  $\mu$  latis, cellulis medianis quatuor fuscis, cellulis terminalibus hyalinis 1-ciliatis; ciliis apicalibus basiliusque similibus, 6–10  $\mu$  longis valde curvatis plerumque ad idem latus versis.

The surface of an infected twig was sterilised by rubbing with alcohol. An acervulus was then picked up, and crushed in a tube containing sterilised water, from which dilution cultures were made in Anar extract agar\*. Plates were incubated at 28° C. As soon as the colonies appeared, these were transferred to plates containing different media, which were examined when fruit bodies had formed. Pure cultures were thus easily obtained.

The germination of the spores was studied in hanging drop cultures in water. Spores germinated after eight to fourteen hours at 26° C.; they swell up by absorbing water, and the cell which gives out a germ tube enlarges and draws nourishment from the adjoining cells. Both the dark and hyaline cells may give out germ tubes. Occasionally two germ tubes emerge from the same cell (Pl. II, fig. iv). The germ tube is hyaline and soon begins to branch. Though no acervuli were formed in the hanging drop, plenty of chlamydospores were formed after six weeks (Pl. II, fig. v). If instead of water, hanging drops of Anar extract are used, germination is more rapid and growth is more profuse.

The spread of the fungus in different media, the effect of different concentrations on growth, the effects of light and darkness, of aeration, of humidity, etc., were studied. Growth of the fungus was observed both in vegetative and synthetic media. Pieces of mycelium from the growing region on agar plates were transferred to the centre of Petri dishes containing various media. These were incubated at 26° C. Measurements of the diameter of the colonies were taken every second day. Table I shows the spread of the fungus in millimetres as well as other growth characters when grown on various media.

The set of inoculated Petri dishes containing different media was kept for seven weeks in order to observe the appearance of fruiting bodies. Table I shows that the spread of the fungus varies considerably, being greatest in Anar extract agar (92 mm.) and least in nutrient agar (29 mm.). Fruit bodies also vary very much in size. In such culture media as water agar, Robinson's medium and nutrient agar, acervuli are absent, whereas in Czapek's synthetic medium and potato extract agar, acervuli were found only on older mycelium in the centre. In Raulin's medium, immature acervuli were formed after three weeks. In the remaining culture media, such as Anar extract agar, rice and maize starch agar, potato glucose agar, Cook's and Richards's media, these were found in groups.

Chlamydospores were observed in potato glucose and Cook's synthetic media.

Cilia are generally of equal length at both ends of the spores, but

\* Anar extract agar, prepared by cooking 100 gm. of Anar (pomegranate) in a litre of distilled water in an autoclave at 1 atmosphere pressure for 20 min., after which it is strained through muslin and made up to 1000 c.c. To this 22.5 gm. of agar is added and the medium is then autoclaved in the usual way.

Table I

			Diameter of hyphae	Zone	
Growth 18 days in mm.		Appearance of acervuli	Cilia 9.5-4.1 $\mu$ Spores without cilia 29.1-22.1 $\times$ 8.8-7.6 $\mu$ Av. 24.3 $\times$ 8.2 $\mu$	2-4 $\mu$ +	
Medium agar	90	5th week, in groups, few	48.2-20.6 $\times$ 41.3-20.6 $\mu$ Av. 34.4 $\times$ 28.9 $\mu$	5.69 $\mu$ +	
Rice agar	74	7th week, very few, scattered	55.0-34.4 $\times$ 48.2-20.6 $\mu$ Av. 45.5 $\times$ 39.3 $\mu$	28.4-25.3 $\times$ 7.6-5.69 $\mu$ Av. 27.5 $\times$ 6.6 $\mu$	9.5-3.8 $\mu$ Av. 6.9 $\mu$ 2-5 $\mu$ +
Maize agar	82	6th week, few pycnidia	41.3-16.5 $\times$ 34.4-16.5 $\mu$ Av. 24.8 $\times$ 22.0 $\mu$	25.3-22.1 $\times$ 9.5-6.9 $\mu$ Av. 24.6 $\times$ 7.6 $\mu$	6-4 $\mu$ Av. 3.16 $\mu$ 3-6 $\mu$ -
Potato glucose	81	4th week, in groups	68.8-27.5 $\times$ 18.2-27.5 $\mu$ Av. 48.2 $\times$ 38.5 $\mu$	28.4-22.1 $\times$ 6.9-5.69 $\mu$ Av. 25.3-6.05 $\mu$	11.1-7.9 $\mu$ Av. 9.2 $\mu$ 1-3 $\mu$ +
Potato extract	68	6th week, very few, on the older portions only	68.8 $\times$ 41.3 $\mu$ Single	25.3 $\times$ 6.3 $\mu$ Av. 25.3 $\times$ 6.3 $\mu$	6.32-5.1 $\mu$ Av. 5.6 $\mu$ 2-4 $\mu$ -
Cook's medium	67	3rd week, comparatively much more numerous than the rest and appear very early	75.6-34.4 $\times$ 61.9-34.4 $\mu$ Av. 55.0 $\times$ 48.2 $\mu$	28.4-25.3 $\times$ 6.9-5.1 $\mu$ Av. 26.9 $\times$ 6.0 $\mu$	6.9-3.16 $\mu$ Av. 6.3 $\mu$ 2-5 $\mu$ +
Czapak's Raulin's	73 78	5th week, one unripe acervulus 3rd week, few unripe only	Absent 34.4-27.5 $\times$ 30.2-24.7 $\mu$ unripe	Nil Nil Nil Nil Nil Nil	Nil 1-3.9 $\mu$ + Nil 2.6-6.3 $\mu$ +
Nutrient agar	29	Nil	Absent	Nil 1-3.8 $\mu$ -	
Richards's	66	4th week, in few groups only	68.8-27.5 $\times$ 68.8-27.5 $\mu$ Av. 46.8 $\times$ 66.8 $\mu$	26.9-23.7 $\times$ 6.9-6 $\mu$ Av. 25.3 $\times$ 6.32 $\mu$	6.9-4.7 $\mu$ Av. 5.69 $\mu$ 1.5-4.5 $\mu$ -
Robinson's Water agar	78 50	Nil	Absent Absent	Nil Nil Nil Nil Nil Nil	2.3-5.7 $\mu$ - Nil 2-4 $\mu$ -

sometimes the difference in length is very great. Their position in relation to the hyaline base is variable; they may be set at different angles and sharply curved. The longest cilia are found on the spores formed on potato glucose. Generally the spores of this fungus are quite big, but on maize starch agar they are small and thin.

A few hyphae running together to form coremial strands is of common occurrence and the growth is zonal in a few cases only, as for example in Anar extract, rice agar, Raulin's, Cook's and potato glucose media.

*Effect of different concentration of media on growth.* For this experiment only Cook's synthetic medium was used. 15 c.c. of different concentrations of Cook's medium were prepared and poured in sterilised Petri dishes. After inoculation these were kept at the room temperature with the day and night variations. The concentrations used were  $N8$ ,  $4N$ ,  $2N$ ,  $N$ ,  $N/2$ ,  $N/4$ ,  $N/6$  and  $N/8$ . The rate of spread of the fungus was studied for over a fortnight, but no difference either in the rate of spread or in the total spread was found at the end of eighteen days. The vegetative growth in higher concentrations was quite characteristic. Pl. II, fig. x shows the striated growth seen in  $8N$  concentrations. It was found that the largest number of acervuli was formed in Cook's normal medium.

*Effect of light and darkness on growth.* Minute pieces of mycelium were transferred to the centre of both vegetable and synthetic media in order to study the effect of light and darkness. Of the four sets of Petri dishes (two sets of Richards's and two of glucose) two sets (one set of Richards's and one of glucose) were wrapped in thick black paper and kept in continuous darkness. Diameters of colonies were measured every second day. Petri dishes kept in darkness were measured in red light inside the dark room. The following table shows the growth measurement in millimetres.

Table II

Medium	Effect of	Days						
		2	4	6	8	10	12	14
Richards's	Light	7	16	24	30	39	43	45
Richards's	Darkness	7	19	25	36	45	54	60
Potato glucose	Light	9	23	36	46	57	66	75
Potato glucose	Darkness	5	23	34	46	60	69	82
								90

The results show that more vegetative growth takes place in darkness than in light. In Richards's medium clear zonation occurs in the dark, but in light, zonation is not so distinct. In potato glucose agar zonation occurs both in light and darkness, but in the light the rings are more compact. In light, fruit bodies were not produced but were formed in darkness.

*Effect of aeration.* For studying this, three sets of four agar plates

were inoculated with the fungus by placing small bits of mycelium from a pure culture in the centre of the Petri dishes by means of a sterilised needle.

One set was sealed with wax so that only limited air was available for the growth of the fungus. The other two sets were also sealed after pouring 18 c.c. of 33 per cent. KOH solution of potassium hydroxide, and 15 c.c. of pyrogallate of potash solution respectively into the lids of the inverted dishes. In the former, growth took place in the absence of carbon dioxide, and in the latter, oxygen present inside the Petri dishes was absorbed by the liquid. These were incubated at 29° C. The following table shows the growth measurement taken in millimeters.

Table III

	Effect of	Days			
		2	4	6	8
I set	Limited air	14	24	36	39
II set	Absence of CO <sub>2</sub>	15	20	22	22
III set	Absence of O <sub>2</sub>	Nil	Nil	Nil	Nil

From the above table, it will be seen that growth in ordinary air containing carbon dioxide is more than in air without carbon dioxide. It seems that the presence of carbon dioxide, though in a small quantity, is beneficial to the fungus. The authors found the same sort of result with another fungus causing a disease of the pomegranates studied by them.

In the absence of oxygen no growth could take place.

The upper thermal death point was also determined by following the bacterial method and was found to be between 47 and 48° C. for an exposure of ten minutes.

*Inoculation experiments.* Perfectly healthy plants were procured from a local nursery. These were kept under observation for over a month before inoculation.

Two plants were kept as controls and others were inoculated either by injection of spore suspensions by means of a hypodermic syringe or by prick inoculation or by spraying with spore suspensions. Three plants were inoculated in each way. A number of cut twigs and leaves was similarly inoculated. Young twigs were cut under water and the cut twigs and leaves were placed in sterilised glass vessels and Petri dishes containing cotton-wool soaked in water or wet filter papers. In all the experiments, before inoculation, the surface of the leaves and twigs was sterilised by rubbing with alcohol. The plants in pots were watered daily and examined regularly. Numerous acervuli were noticed after the third week on the leaf pricked and inoculated with a drop of spore suspension (Pl. II, fig. ix).

The following table shows the result of inoculation experiments:

Table IV

Material	Date of inoculation	Method of inoculation	Remarks on 30. iv. 32
Cut leaves	25. iii. 32	Prickings	Numerous acervuli formed after 4 weeks
„	„	Spraying	No effect
Cut twigs	25. iii. 32	Injections	Abundance of mycelium inside the vessels but no acervuli formed
Plants in pots	25. iii. 32	Spraying	No effect
„	„	Injections	No acervuli observed, though hyphae seen inside vessels*

\* Numerous fruit bodies were present when the material was examined after the summer recess in the following September.

It therefore appears that *Amphichaeta Punicae*, is a weak parasite. It can infect the host only through wounds. Spraying with spore suspension failed altogether to cause infection. Injection methods, though successful, take a long time to show the formation of acervuli, though, when sections were cut, hyphae were observed inside the tissues within a fortnight. Acervuli took a long time to appear on the injected plants in pots; the cut twigs decayed before the acervuli could appear.

#### SUMMARY

A disease of the pomegranate from Lahore, has been described. The fungus causing it is a weak parasite, attacking only nursery plants through wounds. Though the infected plants are not actually killed, they become very much stunted in growth.

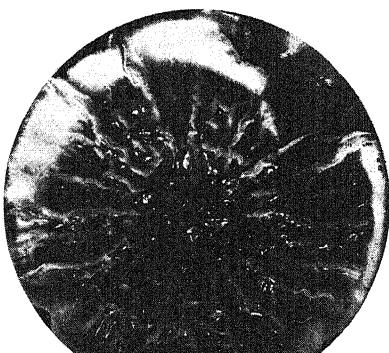
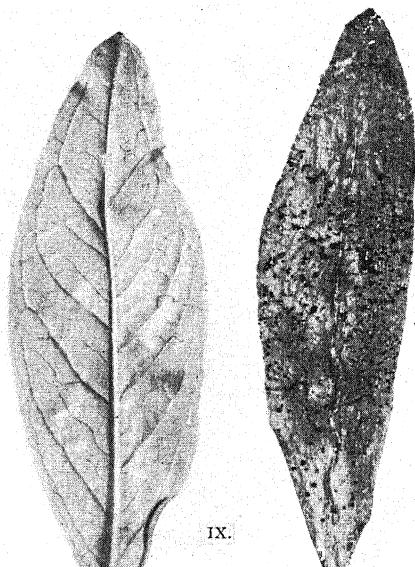
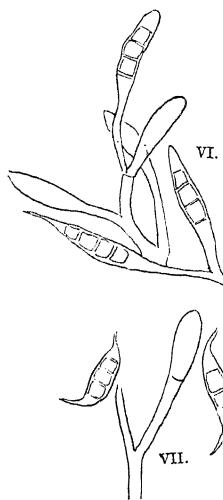
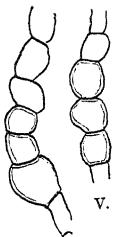
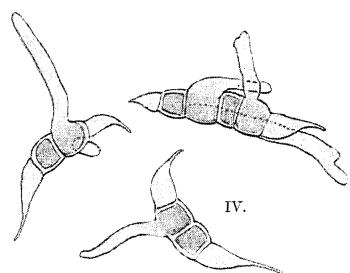
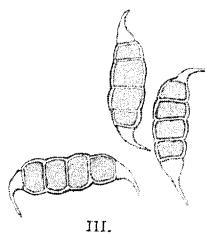
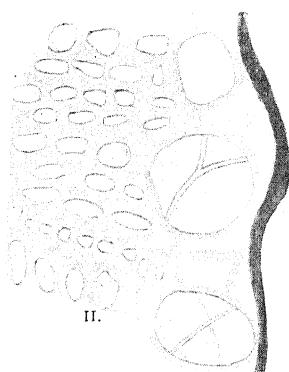
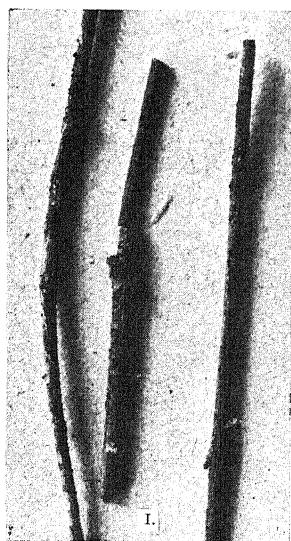
As this species differs considerably from known species of *Amphichaeta*, it has been described as a new species.

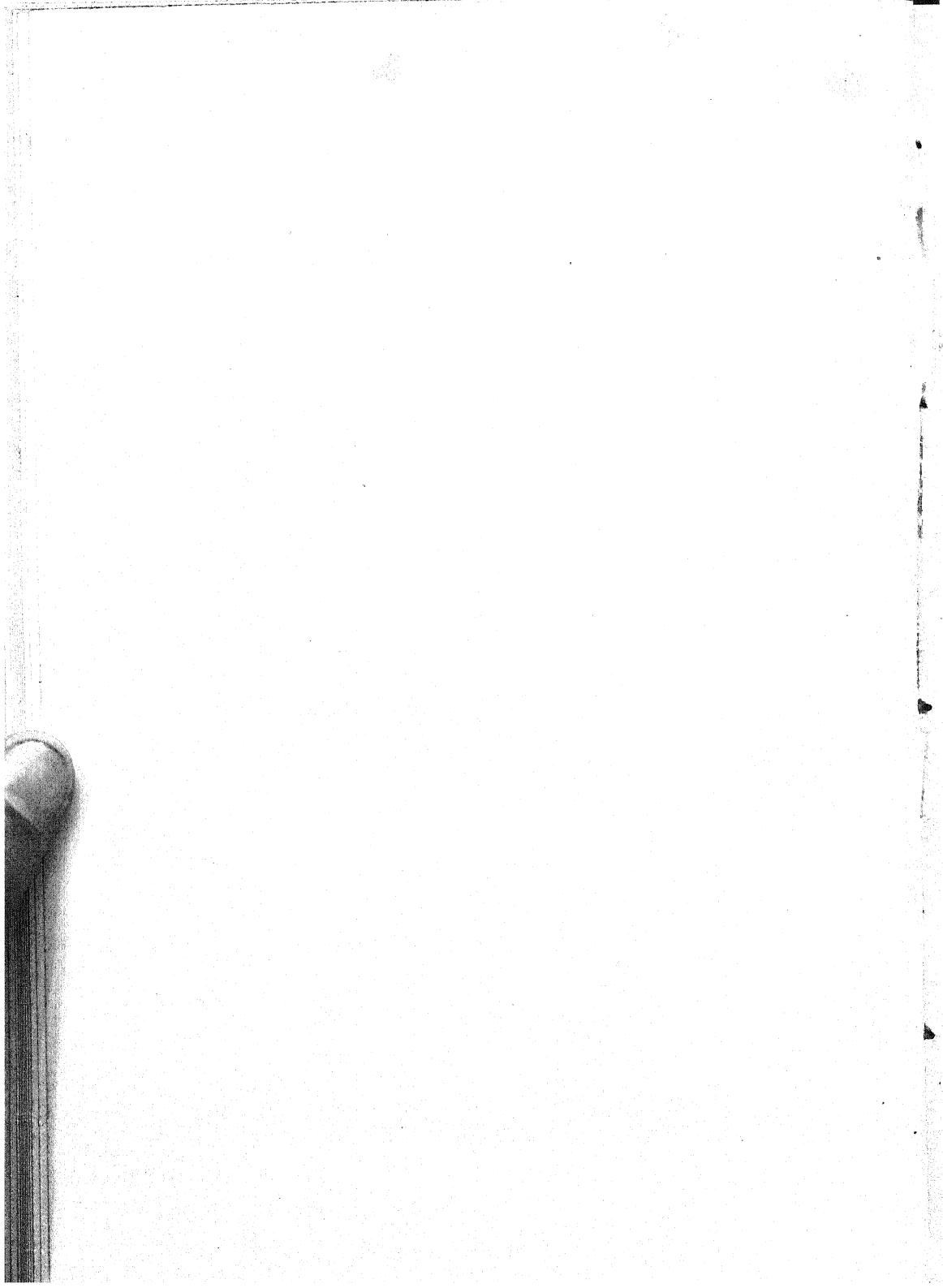
The spores of *A. Punicae* germinate readily in eight to fourteen hours and the fungus will grow on various media. The behaviour of the fungus on different media has been studied as well as the effect of different external factors on its growth.

Though it is a weak parasite, its pathogenicity has been established by means of a large number of inoculation experiments.

#### EXPLANATION OF PLATE II

- Fig. i. Twig showing pycnidia.  $\times \frac{3}{4}$ .
- Fig. ii. Transverse section of twig showing hyphae in the xylem vessels.  $\times 510$ .
- Fig. iii. Spores of *Amphichaeta*.  $\times 510$ .
- Fig. iv. Germinating spores in hanging drops of water.  $\times 510$ .
- Fig. v. Chlamydospore formation in hanging drops, two months' old culture.  $\times 620$ .
- Figs. vi and vii. Conidiophores bearing conidia.  $\times 510$ .
- Fig. viii. Transverse section of a pycnidium.  $\times 120$ .
- Fig. ix. Control and inoculated leaves. The latter bearing numerous pycnidia.  $\times \frac{3}{4}$ .
- Fig. x. Photograph showing character of growth in 8*N* concentration of Cook's medium.  $\times \frac{7}{2}$ .





## A BRIEF ACCOUNT OF FUNGI PRESENT IN THE AIR OVER ORCHARDS, WITH ESPECIAL REFERENCE TO *PLEOSPORA* AND *POLYOPEUS*

By F. M. CARTER

(*Imperial College of Science and Technology, London*)

(With 1 Text-figure)

### INTRODUCTION

IN an investigation on the distribution of micro-organisms in the air, Horne and Nitimargi conducted a systematic exposure of plates of nutrient medium at various localities and made a statistical analysis of the organisms which later developed on the plates. A preliminary account of this investigation has already appeared (8, 9).

This paper deals with the identity of the fungi thus obtained from the air over orchards at East Malling Research Station; at the Horticultural College, Swanley; and in the vicinity of Belfast, Northern Ireland. It forms, in conjunction with the work of Horne and Nitimargi, an attempt to gain further knowledge as to the extent to which decay of apples in storage may be attributed to fungal infection from the atmosphere before the gathering of the fruit.

Special attention has been paid to *Pleospora* and *Polyopeus*, since these fungi, which are definitely known to cause disease of apples, were of such frequent occurrence on the plates.

### CULTURE OF THE FUNGI

The method of trapping the organisms has been fully described elsewhere (8). Individual fungi were isolated from the collection on the exposed plates by subculturing from distinct colonies after a few days' growth.

When bacterial or other contamination was present subculturing on to plates of plain agar was repeated, taking very small inocula from the periphery, until an apparently pure growth was obtained.

It was considered that, for the purpose of this investigation, the advantage of taking monohyphal tip cultures did not justify the labour involved, but monospore isolations were made from a few of the fungi, such as *Pleosphaerulina*, which produce large spores.

Cultures were, in general, maintained on a standard synthetic medium (2.0 gm. asparagine; 0.75 gm.  $MgSO_4 \cdot 7H_2O$ ; 1.25 gm.  $K_3PO_4$ ; 2.0 gm. glucose; 10 gm. starch; 15 gm. agar; 1000 c.c.

water). When reproduction did not occur on this medium potato mush agar, malt extract agar, oatmeal agar and Crabbill's medium (5.0 gm.  $MgSO_4$ ; 1.0 gm.  $K_2HPO_4$ ; 2.0 gm.  $NaNO_3$ ; 0.5 gm. KCl; 0.1 gm.  $FeSO_4$ ; 10 gm. potato starch, 20 gm. agar; 1000 c.c. water) were tried.

#### IDENTITY OF THE FUNGI

Several thousand fungal colonies appeared on the exposed plates in the course of experiment and further culture of the whole number was clearly impracticable but an effort was made to isolate the fungus from at least one colony of each of the different types which occurred.

Identification of the fungi presented a somewhat difficult problem. Lack of knowledge of the natural host, inability to produce ready sporulation, and variation of the organism under cultural conditions all combined to render it rarely possible to state more than the generic position of the fungus.

A list of the genera represented in the collection, with the specific name where possible, is given below.

Nitimargi, who made a preliminary grouping of the cultures into genera, tested many of these fungi on Worcester Pearmain apples, and an asterisk is placed against the name of those which showed an ability to attack the fruit.

Species known to be associated with disease of apple fruit, or, where the specific name is lacking, genera containing such species, are indicated by the addition of references to records of such disease.

#### *List of fungi obtained from the air over orchards*

##### PHYCOMYCETES

*Mucor* (5, 11), *Rhizopus* (1, 5, 7, 11), *Zygorhynchus*.

##### ASCOMYCETES

*Rosellinia*, *Chaetomium*, *Pleosphaerulina hyalospora*, \**Pleospora* spp. (5, 10), *P. herbarum* Pers. ? (10, 16), *Melanospora leucotricha* Corda.

##### FUNGI IMPERFECTI

*Sphaeropsidales*: *Phomopsis*, *Phoma* (1, 5, 10, 11), *Macrophoma*, *Polyopaeus purpureus latirostratus* Horne, *P. purpureus* Horne—other strains (11), \**Polyopaeus* spp. (10), \**Sphaeropsis malorum* Peck, \**Coniothyrium* (5, 10, 11), *Ascochyta* (7, 11), *Diplodia* (11).

*Melanconiales*: \**Pestalozzia Hartigii* Tub.

*Moniliales*: *Oospora abortifaciens* Quek., *Monilia* ( ), *Aspergillus* (11), *Penicillium* (1, 5, 7, 11), *Scopulariopsis brevicaule* Link, \**Eidamia* (7, 11), \**Sporotrichum roseum* Link, \**Botrytis cinerea* Pers. various strains (5, 11), \**Verticillium lateritium* Berk., \**Cladosporium* (7), *C. herbarum* Pers. (?) (11),

\**Stemphylium Berlesii* Oud., *Macrosporium* \**Alternaria* spp. (10, 11) including *A. tenuis* Nees. (?) (5, 11), *A. humicola* Oud. (?) *Stysanus stemonites* Corda (11), \**Epicoccum granulatum* Periz. (5), *Fusarium* spp. (5, 10, 11) including \**Fusarium culmorum* (W. G. Sm.) Sacc. (11), \**Fusarium fructigenum* Fr. (11), \**Trichothecium roseum* Link (1) (*Cephalothecium* Corda).

#### OBSERVATIONS ON *PLEOSPORA HERBARUM* PERS.

A number of different strains of *Pleospora* were obtained from the exposed plates and were identified at the British Museum (Natural History) as strains of *P. herbarum* Pers.

Ellis (3) and Rose and Butler (16) record a *Macrosporium* conidial stage of *Pleospora herbarum*; Machacek (12) has identified *Macrosporium parasiticum* and *Pleospora herbarum* as stages in the life history of one fungus which causes spot on onion stems, and Kidd and Beaumont (11) have stated that the conidial stage of the *P. herbarum* which they found on apples was *Macrosporium commune*. The conidia produced in the early cultures of the strains now under consideration were of the *Stemphylium* type, but they ceased to be formed before their connection with the perfect stage had been established.

Perithecia were formed in abundance in most of the cultures, but the proportion which proved fertile was low. Some strains never produced ascospores but were placed in this group on account of their general appearance and the presence of black bodies resembling immature perithecia.

Some of the originally fertile strains became sterile later, possibly as a result of repeated subculture on the standard medium, since Newton (13) refers to the tendency of other species of *Pleospora* to lose the power of producing perithecia when cultures on a rich medium are frequently renewed.

Table I summarises the cultural characters of the various strains of *P. herbarum* investigated. Since cultures of the different strains were most distinct from each other on the standard medium but most fertile on oatmeal agar, descriptions of vegetative characters relate to standard medium cultures while perithecial characters are those observed on oatmeal agar.

The descriptions of the colours produced in the medium follow Ridgway's system of nomenclature (15).

The reaction of a number of the strains to addition of acid to the medium has been dealt with elsewhere (2). The radius of spread of each strain after nine days' growth at 20° C. in standard medium containing 0.0, 0.25 or 0.5 per cent. malic acid is given in Table II.

The strains were also tested on Worcester Pearmain apples. Inoculation was performed as described by Granger and Horne (4). Each strain was used to inoculate ten apples and each apple was

Table I. *Pleospora Herbarum*, Strains 1-16. *Vegetative characters on*

Strain	Colour produced in standard medium	Colour produced in oatmeal agar	Outline of growth	Colour of mycelium	Type of growth
1	Yellowish	None	Regular	White	Silky aerial mycelium with even surface
2	"	Pale yellow-orange	"	"	Woolly aerial mycelium with uneven surface
3	"	"	"	"	Prostrate in parts. Woolly aerial mycelium snow-like appearance
4	"	Honey-yellow	"	Greyish white	Woolly, snow-like. Darker at centre
5	Yellowish with some black	Pale yellow-orange	"	White to greyish	Short, woolly. Thicker at centre. Margin transparent
6	"	Honey-yellow	"	"	Fluffy at centre, less thick at margin
7	"	Pale yellow-orange	Irregular	"	Slight, hirsute growth
8	Pinkish yellow with some black	Ox-blood red	Regular	Greenish grey	Short, silky mycelium. Centre darker than margin
9	"	"	"	"	Erect, silky. Centre darker than margin
10	"	None	"	Grey	Short, woolly mycelium
11	"	Ox-blood red	"	Greyish white	Compact. Margin transparent
12	Pinkish yellow with some black at centre	Salmon-pink and pale orange-yellow	"	"	Spreading. Fluffy in patches. Thicker at centre
13	Pinkish yellow with some black	Ox-blood red	Indefinite first. Regular later	"	Spreading. Fluffy in patches
14	"	None	Lobed	"	"
15	Orient-pink	Salmon-pink and pale orange-yellow	Regular	White	Silky mycelium. Margin transparent
16	"	Ox-blood red and vinaceous	Stellate	"	Silky mycelium almost prostrate. Narrow transparent marginal zone

*Brown's synthetic medium. Perithecial characters on oatmeal agar*

inoculated with three strains, at different equatorial points. All the strains tested were found capable of attacking the fruit. The rot was estimated twenty days after inoculation by weighing the apple before and after removal of the decayed tissue from each infected area in turn. From the data obtained, the radial advance of each strain was calculated and the resulting values are also shown in Table II.

It will be observed that the strains differ in activity both in synthetic media and in the apple fruit.

Table II. *Pleospora herbarum. Relative activity of thirteen different strains in apple fruit and in standard medium varying in malic acid content*

Strain	Radial advance in apple fruit (mm. after 20 days at lab. temp.)	Radius of spread (mm. after 9 days at 20° C.)		
		0·0 % acid	0·26 % acid	0·5 % acid
10	2·0	34·0	27·5	18·0
9	1·8	36·0	25·0	22·0
12	1·1	33·5	14·0	9·0
7	1·0	25·0	16·0	12·5
2	1·0	34·0	29·5	22·5
5	0·9	30·5	20·5	14·5
16	0·9	35·0	26·5	17·0
15	0·9	37·0	13·5	17·5
1	0·6	30·0	16·0	12·0
3	0·5	29·0	21·0	13·5
4	0·5	31·5	21·0	14·5
8	0·4	32·0	17·5	19·5
13	0·3	20·0	12·5	6·5

#### OBSERVATIONS ON *POLYOPEUS* spp.

Colonies of *Polyopeus* appeared on nearly every exposed plate. Many were easily recognisable as strains of *P. purpureus* Horne(6); others could not be placed with certainty in any existing species. Several of the latter forms, numbered for convenience *Polyopeus* 1-8, were grown on Crabill's medium in which pycnidia rapidly developed. The various types of pycnidium are illustrated in Fig. 1, while the cultural characters of the fungi are given in Table III.

It will be observed that the pycnidia differ considerably in size, shape and colour, and the necks are diverse in colour and appearance but any particular culture was consistent in the type of pycnidium it produced.

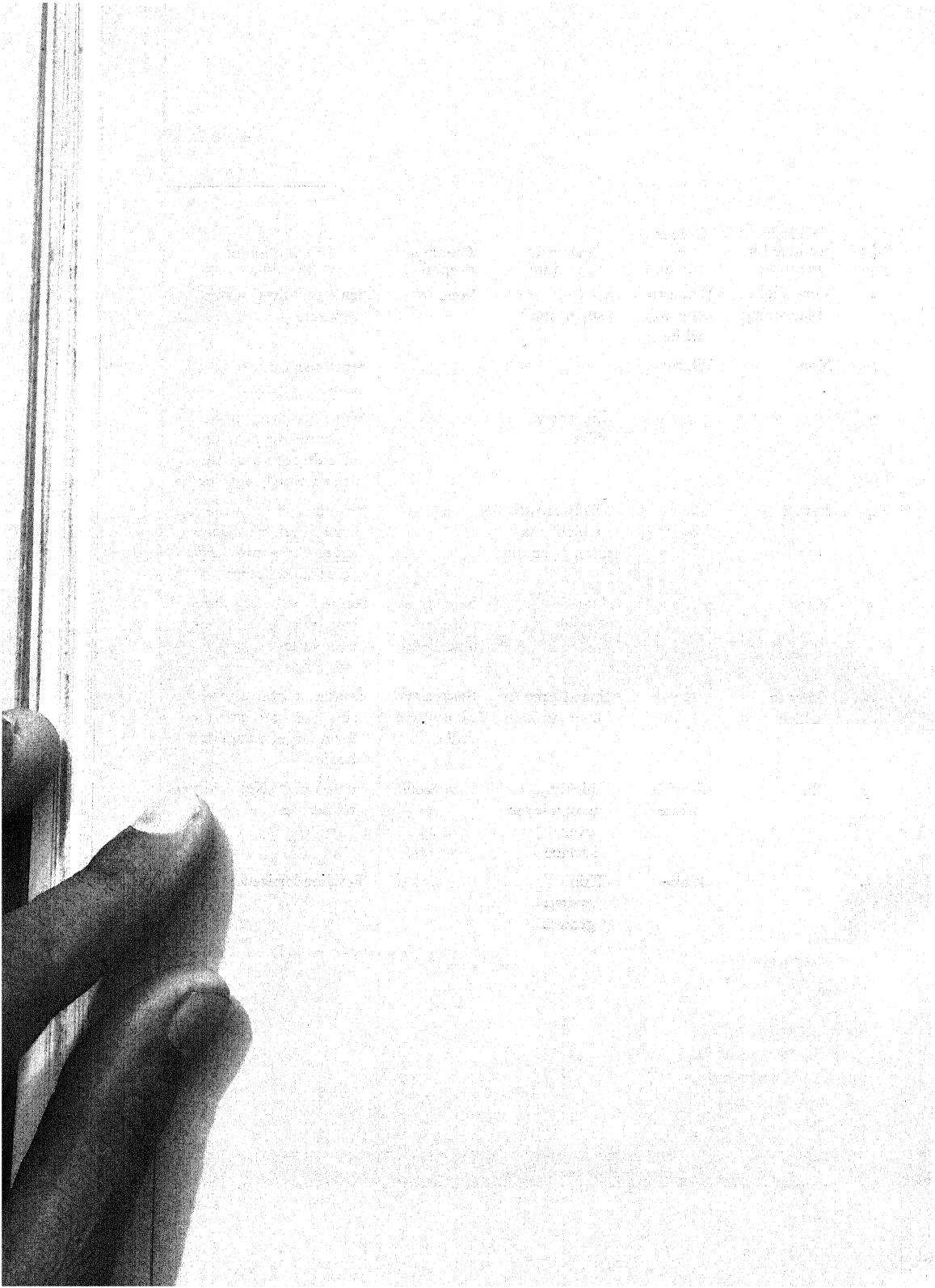
*Polyopeus* 2 has been grown on media varying in carbohydrate and malic acid content as described in another paper(2), where it is shown that acid retards growth to an extent dependent on the concentration of carbohydrate. Data illustrating this point are reproduced in Table IV.

Table III. *Polyopeus spp. Characters on Crabb's Medium*

<i>Polyopeus</i>	Pycnidia												Length of hyaline spores (in $\mu$ )	<i>Polyopeus</i>
	Colour produced in medium	Colour of mycelium	Nature of mycelium	Chlamy-dospores	Distribution of Pycnidia	Depth in medium	Dimensions of body (in $\mu$ )	Colour of body	Type of opening	Number of openings	Colour of neck	Dimensions of neck (in $\mu$ )		
1 Very slight blackening	White to brownish white	Sparse, superficial	None	Scattered over surface, separate	Seated on surface	148×130 to 259×240	Black	Neck sometimes slightly curved	1 or 2*	Brown	110×93	4·6	1	
2 None	White	„	„	Scattered over surface, mostly separate	Slightly embedded	167×93 to 225×185	„	Slender necks, straight or bent	1 usual, occasionally 2 or 3	Black	Up to 167×55	5·2	2	
3 „	„	Superficial film	„	Scattered over surface, separate except at limit of culture where they are crowded together	„	Up to 400×400	Hyaline-brown-black	Necks lying parallel to surface	1-7	Dark brown or black	Up to 370×95	4·5	3	
4 Purple	„	Fluffy growth which may cover pycnidia	„	Scattered over surface, usually single, some aggregated into large compound bodies	„	220×200 to 440×370	Hyaline	Short neck or ostiole	1 usual. Multiple ostioles where pycnidia join	Black	Ostiole diam. 40-50	6·8	4	
5 Black	„	Sparse, aerial	Numerous brown unicellular	Aggregated into large, irregular groups all over surface	Base slightly embedded	Single 185×185. Group of 8, 460×370	Hyaline-light brown	Irregular necks, bent, occasionally branched	1-several	Hyaline at base. Black at tip	Length up to 315. Width up to 130	4·3	5	
6 Grey to black	„	Sparse growth over surface	Some at bottom of tube	Scattered over surface, single or aggregated to form large, compound bodies	Seated on surface	185×185 to 315×240	Hyaline	Short necks or ostioles	Openings may be confluent where pycnidia join	Black	55×46. Ostiole diam. up to 55	4·3	6	
7 Black	Greyish white	Thickly woven layer over surface	Numerous	Scattered. Not very numerous	Sunk in medium	130×90 to 260×90	Black with lighter areas	Indication of neck each end	1 or 2	Black. Lighter at tip	—	No spores	7	
8 „	White	Thin matted growth	„	Few, undersized	„	—	Black	Slight indication of short wide neck	1 or 2	Slightly less dark than rest of pycnidia	—	No spores	8	

\* One neck found with two openings, see Fig. 3.

*Trans. Brit. Mycol. Soc.*, facing p. 150.



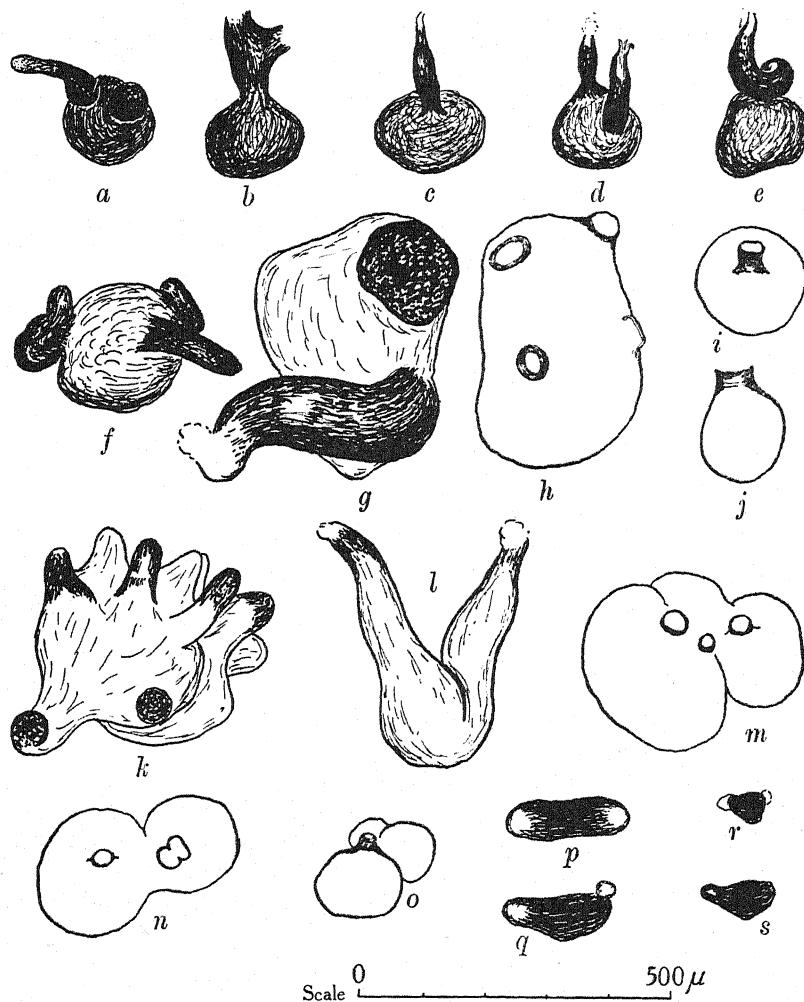


Fig. 1. *Polyopepus* spp. Pycnidia formed on Crabill's medium. *a, b*, *Polyopepus* 1; *c, d*, *Polyopepus* 2; *e, f, g*, *Polyopepus* 3; *h, i, j*, *Polyopepus* 4; *k, l*, *Polyopepus* 5; *m, n, o*, *Polyopepus* 6; *p, q*, *Polyopepus* 7; *r, s*, *Polyopepus* 8.

Table IV. *Polyopepus* 2. Radius of spread (mm.) after nine days' growth in media varying in carbohydrate and malic acid content. 20° C.

Carbohydrate	Nature	%	Malic acid %		
			0.0	0.3	0.6
Glucose		0.2	27.0	21.0	13.0
		9.0	44.0	20.0	11.0
		12.0	26.0	11.0	10.0
Sucrose		17.1	20.3	8.0	0.0

*Polyopeus* is one of the commonest causes of "spots" which develop in apple fruit at a late period in the season (7, 10, 11), and it is worthy of note that all the strains mentioned have been proved to be capable of developing in Worcester Pearmain apples.

#### DISCUSSION

The range of genera represented by the fungi which settled from the air over orchards is wide but, as pointed out by Horne (8), the colonies which appeared on the exposed plates do not necessarily include every species falling on the plates. Some fungal spores may be unable to develop on the particular medium used, others may be incapable of growth on any artificial medium, while others again, may require a period of rest before germination.

These facts probably account for the absence of Basidiomycetes and the preponderance of Fungi Imperfecti which, in general, are tolerant of most media.

It is noticeable that all but a few genera on the list have been recorded as occurring on apple fruit, but it must not be assumed that the unnamed species belonging to genera which contain some pathogenic members, are, without exception, those species which are responsible for disease.

It is also interesting to note that some species such as *Sporotrichum roseum* and *Verticillium lateritium*, although not previously isolated from apples, have been found capable of attacking the fruit when artificially introduced.

While most of the fungi listed in this paper are known to occur on apples, the converse is also true, that the majority of the fungi isolated from diseased apples at all stages of maturity appear on the list. Hence it seems reasonable to conclude that apple rots in storage, are, to a great extent, due to fungal infection from the air before picking.

Horne (8) has shown that the number of fungi present in air over an apple orchard at Exning, Cambridgeshire, far exceeds that in air over orchards at East Malling. He also points out that the East Malling crop suffers much less from fungal attack in storage than does that from Exning, although resistance to fungal invasion after artificial inoculation is actually less in East Malling apples than in those from Cambridgeshire. Further evidence in this paper of the pathogenic nature of the fungi obtained from air over orchards supports Horne's suggestion that absence of infection rather than peculiar powers of resistance may account for the freedom from storage disease shown by apples from localities such as East Malling.

### SUMMARY

A list is given of fungi which settled on plates exposed to the air over apple orchards, together with references to records of their pathogenicity towards the apple fruit.

Several strains of *Pleospora herbarum* Pers. are described and some forms of *Polyopanus* Horne which could not be ascribed to any known species are briefly recorded.

It is suggested that disease of apples in storage is chiefly due to fungal infection from the atmosphere before the gathering of the fruit.

The author wishes to thank Dr A. S. Horne for his help throughout the work, Prof. V. H. Blackman for his interest and criticism, and Miss F. L. Stephens, British Museum (Natural History), South Kensington, for kindly identifying a number of the fungi.

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## NOTE ON THE ISOLATION OF SINGLE SPORE CULTURES

By DIN DAYAL GUPTA, B.Sc. (AGR.)  
(*University College of Wales, Aberystwyth*)

(With 1 Text-figure)

THE difficulty of isolating single spores has been appreciated by mycologists, and small spores, such as the conidia of *Eurotium herbarium*, provide special difficulty. During a study of the cytology and physiology of this fungus, it became necessary to investigate the phenomenon of aversion.

For this purpose single spore cultures were essential. A simple technique was developed to isolate single spores of *Eurotium* and this method, described below, was found to be effective, the chances of contamination being practically obliterated.

### DETAILS OF THE TECHNIQUE

Capillary tubes (diameters 0.5-0.75 mm.) were drawn from clean glass tubing. Each capillary tube was drawn to a very fine aperture at one end and sealed off; the other end was also sealed by quickly putting it into the flame and drawing rapidly.

The resulting capillary tube (Fig. 1 a) was perfectly sterile, the total length of the tube being ten to twelve inches. The tube was then bent in the middle at an angle of from 30 to 45° by rapidly passing it through the flame of a fish-tail burner.

The capillary tubes are difficult to bend in a large flame, in which they may collapse. Dr B. Barnes has therefore suggested the use of a "micro-flame" which consists of a glass tube with a jet having a very fine aperture. This tube is attached to the gas outlet with a length of rubber tubing. The small flame (= "micro-flame") is extremely useful, both in closing the ends of the capillary tubings and bending them.

A spore suspension was made in a test-tube containing sterilised water. The outside of a capillary tube was sterilised by means of alcohol over the surface (with care, these tubes can be sterilised in the auto-clave). As soon as the alcohol had evaporated the test-tube was opened and the A end of the tube (Fig. 1 a) immediately pushed into it and the plug was replaced. This end was broken by tapping the tube against the bottom of the test-tube. As soon as the tube was

broken at the other end the suspension rapidly travelled up, and completely filled the tube, but the free end being so fine, the suspension could not drop (Fig. 1 b). When this end was touched to any surface, a tiny drop emerged. On examining drops on slides under the microscope, it was found that most of them contained a single conidium.

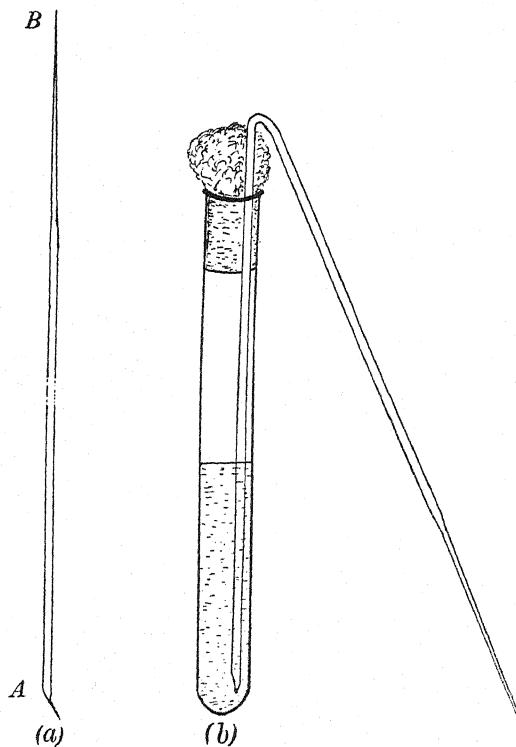


Fig. 1. (a) Capillary tube closed at both ends *A* and *B*. After bending the end *A* is put in test tube; both ends are broken. (b) Test-tube containing conidial suspension in sterilised water. Capillary tube is in position, and the apparatus is ready for sowing suspension drops.

Petri dishes containing sterilised agar-agar were marked underneath with ink-dots. The suspension drops were sown over these dots and the dishes were incubated at 33° C. to favour germination. Isolation of individual conidia before germination was found to be practically impossible (search for them being in vain).

Later, it was found that the usual medium (prune agar) was more

satisfactory than pure agar for sowing the suspension drops as germination was more rapid upon it and further growth more satisfactory. After twenty-four to thirty hours the dishes were examined under the microscope and single germinated conidia were isolated with the help of a dummy objective\*.

To minimise the chances of contamination it was found useful to sow a single suspension drop in the centre of a Petri dish and isolate the young germinated conidia.

The drop spreads out quickly, so that if it contains more than one spore they separate out and give sufficient room for isolation.

The free end of the capillary tube was sterilised with absolute alcohol every time it was used.

\* De la Rue, C., "Isolating single spores." *Bot. Gaz.* LXX (1920), 319.

## PROCEEDINGS

Meeting held at University College, London, March 17th, 1934,  
Dr B. BARNES, President, in the Chair.

### E. M. BLACKWELL. The Germination of Oospores of *Phytophthora Cactorum*.

After a citation of the few definite records of germination of oospores of *Phytophthora* spp., a method of refrigeration was described by which profuse germination of oospores of *P. Cactorum* had been obtained at will during the winter 1933-4.

A possible explanation was then offered of the action of the various mechanical, physical and chemical agencies that have in the past been used to induce germination of resistant spores of fungi, viz. cracking of the spore membrane, heat, cold, drought, "nutrients," volatile substances, acidity,  $\text{CO}_2$ .

The following facts were considered:

(1) That a resting spore is a colloidal complex of protoplasm and reserves enclosed within an almost impermeable membrane of fungus cellulose also colloidal in structure;

(2) that during dormancy of the spore these colloids are at their iso-electric point: the point at which they hold a minimum of "bound" water;

(3) that it is upon the enclosing membrane that the various agencies work: the protoplasm and reserves coming into play later when germination is initiated and the conditions for germination secured.

It was suggested that the effect of the physical agencies upon this resistant membrane would be to bring about a permanent change in the configuration of its colloidal system, thus forming cracks through which water and gases could pass; and that the various chemical factors might all bring about a change in the  $\text{pH}$  of the colloids thereby inducing swelling and so producing intermicellar spaces through which water and gases could pass.

Since many observers have found that a period of "after-ripening" is enough in itself to induce germination, it was further suggested that since  $\text{CO}_2$  tends to accumulate within a resting spore there would ultimately come a moment when this would add an electric charge to the colloids and the resistant wall might be rendered permeable from within.

### E. H. ELLIS. Preliminary Observations on Mycorrhiza.

Continuous field and laboratory observations over long periods on the seasonal variation of the mycorrhiza of *Pinus sylvestris* and *Larix decidua* suggest that the association of tree and fungus is obligate to the trees beginning in *Pinus sylvestris* in the seedling stage. Experimental addition of a mixed infection produced a marked increase in growth rate resulting in the production of giant seedlings. So far as can be ascertained, infection of a young root normally occurs during late autumn when the mycelia of Basidiomycetes are active and small brown knots of neoplastic growth are formed on the roots. In the following spring when growth of tree roots in the humus layer once more becomes active, these knots are enlarged and become bright pink. During summer the close knot of rootlets is separated by a rapid longitudinal growth giving rise to the coraloid root that has so often been described, and in early autumn this phase is succeeded by one in which the coraloid triangles become draped with a loose mesh of mycelium. Usually during late summer and early autumn it can be seen that the normal direction of growth of lateral roots is reversed and they grow upwards from soil into the humus layer and

there become infected by fungi. No suggestion is offered on the influences responsible. Observations of other workers are confirmed that Hymenomycetous fungi are concerned in the association. Species of *Boletus* are principally found on *Larix decidua*, but there is a more mixed range, frequently with *Marasmius peronatus*, on *Pinus sylvestris*. Animal activities, notably those of mice and beetles, are thought to be important factors conditioning the growth of the fungi. Insufficient evidence is available to understand the nature of the symbiosis, but the old distinction of ecto- and endo-trophic mycorrhiza is thought to be more descriptive than actual and may be seasonal. The fungus commonly penetrates the cortical cells of roots but seems unable to pass beyond the endodermis to the stellar region. The "Hartig net" is a pseudo-parenchyma of hyphae. The fungus mantle of larch sometimes shows on its outer surface small spines that abstract microconidia. It is hoped these may prove to be Hymenomycetous conidia.

### J. B. HAMOND. A Graft Disease of Walnuts caused by a Species of *Chalaropsis*.

In 1930, a fungous disease caused an almost complete failure of the walnut grafts at the East Malling Research Station. Brown spores, found in abundance on the cut surfaces of the diseased stocks and scions, were isolated in pure culture, where they gave rise to chains of hyaline endospores. These endospores, in conjunction with the brown macrospores borne singly and terminally, indicated that the walnut graft fungus belonged to the genus *Chalaropsis* of Peyronel.

Three other strains of *Chalaropsis*, isolated for comparison, were obtained from a walnut root, carrots and peach seedlings respectively.

The four strains of *Chalaropsis* all bear a general morphological resemblance to one another. When growing freely, most of the mycelium is in the form of endoconidiophores consisting of one to four cells terminating in a tapering endoconidial cell. The macroconidia are sessile, or borne on unicellular conidiophores. In slowly growing *Chalaropsis* cultures, very thin, vegetative mycelium, with intercalary swellings appears in profusion. The strain isolated from carrots may be distinguished from the other strains by its macrospores which are almost spherical, instead of ovoid, and by the fact that the endospores are olive-green when seen in mass.

The cultural relations of these fungi have been studied by growing them on various media. It was found that the fungi tend to form a series, at one end of which is the walnut graft strain, usually forming cultures which are light-coloured and regular in outline, while the carrot strain, at the other end of the series, produces typically fringed growth, which is dark green or nearly black. The other two strains are intermediate.

The type of growth obtained at different temperatures was studied for each of the four strains and differences in the response of each strain to temperature, suggested an adaptation of the fungus to the environment of its host. The type of growth obtained at various degrees of acidity was also studied, and tests were applied for the more important enzymes.

On young walnut trees, the fungus always enters through a wound or at a cut surface, and seems unable to penetrate the uninjured epidermis. Sections through diseased stocks and scions, showed spores all along the cut surfaces, and mycelium in all types of cell. Naturally infected tap roots showed varying degrees of disintegration of the tissue, beginning at the cut surfaces.

Inoculations on walnuts at the time of grafting, yielded positive results, artificially inoculated plants being indistinguishable from those which had become naturally infected. None of the strains of *Chalaropsis* resulted in much damage when inoculated into shoots of established walnut trees, all lesions eventually healing normally. Striking differences in degrees of parasitism were shown when the four strains of *Chalaropsis* were inoculated into carrots, the fungus isolated from this host being the most parasitic. When the *Chalaropsis* strains were inoculated into lupin seedlings (the host on which *C. thielavioides* was originally recorded in Italy), there

was very little damage, the plants continuing to grow normally. Throughout these series of inoculations, no injury resulted from the fungus unless the epidermis of the host was injured.

Laboratory tests in the control of *Chalaropsis* have shown that formalin is highly toxic to the macrospores. As formalin can be conveniently manipulated, it is now generally used to control the walnut graft disease at East Malling.

These four fungous strains bear a general resemblance to *C. thielavioides* described by Peyronel. Until the perfect stage is discovered, therefore, it is proposed to adopt the name *C. thielavioides* for these strains. In view of Peyronel's work on *C. thielavioides*, it seems very probable that the two fungi described under different names by McAlpine in his *Fungous diseases of stone-fruit trees in Australia, and their treatment*, should also be relegated to the genus *Chalaropsis*, and described as one fungus. Also, macrospores similar to those found on walnut grafts, have now been identified on some walnut shells in the Herbarium at Kew. Previously, endospores only had been recognised on these shells. This indicates that *C. thielavioides* was present in Britain before it was found on diseased walnut grafts.

#### J. RAMSBOTTOM. Fragmenta Bibliographica.

The volumes shown were a copy of Sowerby's *English Fungi* with the original wrappers (cf. *Trans. Brit. Mycol. Soc.* xviii (1933), 167-70); a supplement to Fries's *Systema Mycologicum* (1830) (cf. tom. cit. p. 316); and two copies of Persoon's *Synopsis Fungorum*, one of these from the library of the Linnean Society of London and formerly in the possession of J. E. Smith, having a couple of cancel pages, one with the description of a genus *Bungea* afterwards replaced by *Batarrea* (photograph in *Proc. Linn. Soc. Lond.* cxlvii (1933), 15-16), the other showing that the two parts of the *Synopsis* were published as one volume.

#### E. M. WAKEFIELD. Exhibit of fungi from British Guiana.

## REVIEW

*The Genus Diaporthe Nitschke and its segregates.* By LEWIS E. WEHMEYER. Pp. 349, with xviii plates. Ann Arbor, University of Michigan Press, 1933.

It has been generally known that Dr Wehmeyer has been engaged for some years on a monograph of *Diaporthe* and all mycologists will welcome its appearance. The author begins his preface:

"The description of new species and genera is no longer the chief purpose of systematic mycology. In many groups, particularly in the Ascomycetes, the numerous incomplete or inadequate and scattered descriptions of species and genera have accumulated as an undigested mass of material, which makes the description of new species and genera in these groups extremely hazardous. Confusion in the taxonomy and the literature also renders insecure ecological or distributional deductions from these data.

"It is extremely important, therefore, in order to advance our knowledge of the taxonomy, phylogeny, and biology of these groups and to put it on a firm basis, that there should be a careful comparative study of the collections and data already amassed, so that they may be reorganized into a workable and related whole."

With this probably everyone would agree, though many would object to the first sentence. I, for one, hold very strongly that "species-mongering" has never been the chief purpose of systematic mycology.

Monographic study of the kind here presented is an urgent need, but unfortunately few have the time or the opportunity to accomplish it. The intensive knowledge gained by going over the whole field gives a feeling of taxonomic security which otherwise is wanting. The present study is "based on material actually seen and examined." The Introduction occupies thirteen pages and deals plainly and concisely with the points at issue. From it we learn that 650 species have been ascribed to the genus *Diaporthe* founded by Nitschke in 1867 [1870]. About a hundred of these are either wrongly or doubtfully placed, and many others fall into synonymy. Some genera have been segregated and those adopted and treated in the present work are *Apioportha*, *Diaporthopsis*, *Diaporthella* and *Cryptodiaporthe*. (*Diaporthella* was proposed by Petrank in 1924. It includes a few species characterized by the very strongly developed erumpent stroma.)

The treatment of the species is on the same lines as in the author's paper in the *Transactions* (xvii (1933), 237-95). The species are separated on purely morphological grounds and little or no weight is placed on host-relation. Dr Wehmeyer has had much experience in growing these fungi in culture and consequently speaks with authority but I feel that he has been somewhat ruthless and will not be followed in several of his suggestions. The erection of "species" in *Diaporthe* has been somewhat like that in *Fungi Imperfici*—a new host a new species—with usually no attempt to point out its morphological similarities. But the account of *Diaporthe Arctii* occupies twenty pages: the species is described and one variety—the rest of the space is occupied with the description of the fungus on over twenty different hosts and the sinking of names for both the perfect and conidial stages. Similarly *D. pardalota* occupies twenty pages and *D. eres* thirty.

There can be no doubt that the author has done most valuable work in arranging so many forms under a species of wide extent. Whether he is right in assuming that the differences are merely due to the host remains for future investigations to show for we know little about the host limitation. From the grouping, clues to several problems are apparent and it is to be hoped that these will soon be followed up, for it is certain that we now have a sure foundation.

The book is well produced and has a workable index. It is worthy of a fuller and more critical notice than can be attempted here, for it gives the results of a very arduous investigation.

J. R.

## NOTES ON ENTOMOGENOUS FUNGI

By T. PETCH

(With 7 Text-figures)

76. *CORDYCEPS ENGLERIANA* P. Henn.

*CORDYCEPS ENGLERIANA* was described by Hennings in 1897 (*Engl. Bot. Jahrb.* xxiii, 539) from a specimen on a spider from the Cameroons. From the host arose numerous slender clavae, up to 15 mm. long, some of them conidial and others perithecial. The conidial clavae were branched above, blackish brown, and bore oblong basidia,  $6-7 \times 3.5-4 \mu$ , with ovoid-ellipsoid, hyaline conidia,  $4-5 \times 3-3.5 \mu$ . The perithecial clavae were blackish below and yellowish ashy above. The perithecia were situated in a cluster on one side of the clava at the apex, and were superficial, cylindric, fusiform, with an obtuse, rounded apex, 1-1.5 mm. high and 0.25 mm. diameter. Hennings stated that the perithecia looked like small insect pupae.

The foregoing details are taken from Hennings's description. The type is now preserved in alcohol as an exhibition specimen. The specimen conforms to Hennings's description and figure, but further details of the conidial stage cannot be obtained. The perithecia are superficial, elongated oval or cylindric.

From Mr A. W. Bartlett, I have received a British Guiana specimen which appears to be this species. The host is a large spider, seated on the leaf of a Monocotyledon. From the body and legs of the spider, there arise twenty-one clavae, scattered or sometimes two together. The clavae are up to 15 mm. high, linear, variously twisted and curved, sometimes forked above, blackish brown or black. Some clavae are conidial, and bear cylindric basidia,  $18 \mu$  high,  $3 \mu$  diameter, continuous or one-septate, rounded and thick-walled at the apex, with a minute, central sterigma. This is evidently a *Hymenostilbe*, but conidia were not found. The perithecial clavae are slightly thickened towards the apex, and there bear the perithecia along one side, usually clustered, with a few outlying scattered. The perithecia are 0.6 mm. high, 0.3 mm. diameter, superficial, elongated ovate or slightly flask-shaped, apex obtuse. The asci are  $5 \mu$  diameter (not  $8-10 \mu$ , as given by Hennings), and the fungus is a *Cordyceps*, not *Ophiocordyceps*. The specimen is an old one, and the perithecia are now brown, the wall being red-brown by transmitted light.

The spider is attached to the leaf by a fringe of tawny brown mycelium

along its legs. In the type specimen, the spider appears to be merely clasping a stem, without any mycelial attachment, as far as can be determined by inspection through the glass of a museum jar.

In 1901, Möller (*Phycomyceten und Ascomyceten*, p. 208, fig. 97) figured and briefly described *Cordyceps flavo-viridis* from Brazil. This species was found on the leaf of a *Calathea*, on which it formed a closely adpressed, fleecy, loose stroma, arising from some small brown pupae. From the stroma, densely interwoven, greyish white strands, about 1 mm. broad, extended over the leaf in various directions, and on these strands were situated superficial, elongated flask-shaped, yellow-green perithecia, 0.5 mm. high, singly or in groups. Möller believed that the fungus was parasitic on the brown pupae, two of which are shown in his figure.

Inspection of the type specimen, through the wall of a museum jar, causes some doubt of Möller's interpretation. The repent strands appear to arise from a mass of debris, which is apparently situated beneath a thin silk sheet, such as is constructed by a spider on the under surface of a leaf. When a spider beneath one of these tents is killed by a fungus, the fungus grows out, sometimes through the silk sheet, but more usually along its margin, which is not attached to the leaf all round. Moreover, other insects may take refuge underneath the sheet, and a dead spider is often devoured by scavengers. In the type specimen of *Cordyceps flavo-viridis*, the minute pupae appear to be quite clean and not attacked by the fungus. It would seem probable that these are the pupae of some intrusive insect, perhaps a Dipteron, and have no relation to the fungus.

Möller remarked that *C. flavo-viridis* was a *Torrubiella*, according to the definition of the latter genus, but if the repent strands which bear the perithecia were only a little more firmly compacted, so that they could stand erect, the difference between *Cordyceps* and *Torrubiella* would disappear.

In that case, however, the fungus would be *Cordyceps Engleriana*, with which its large free perithecia agree. I suggest that *C. flavo-viridis* is a small example of *C. Engleriana*, and that it is parasitic on a spider, not on the pupae which occur in the mass of mycelium. That can be decided only by examination and dissection of the type specimen.

In *Mycological Notes*, No. 69 (July, 1923), p. 1197, C. G. Lloyd wrote, "Isaria flavo-viridis from Rev. J. Rick, Brazil (fig. 2445). As named by Rev. Rick, or rather as *Cordyceps*, but I would rather record it as *Isaria* until its *Cordyceps* nature is proved. The name is quite appropriate to express its color. Growing on a pupa it no doubt is a *Cordyceps* or will develop into one. I do not like to cut the only specimen, but on scraping it I find only greenish hyphae. No sign of perithecia or even conidial spores." The figure shows an erect

cylindrical clava growing from a pupa and has no resemblance to Möller's illustration. This is probably a case of the inadvertent use of a prior name.

### 77. *CORDYCEPS AINICTOS* Möller

In *Phycomyceten und Ascomyceten* (1901), Möller described, under the name *Cordyceps ainictos*, a peculiar specimen which appeared to have two different kinds of perithecial clavae arising from the same insect. In the one kind, the perithecia were totally immersed in a lateral pulvinate head; in the other, they were completely superficial on long linear clavae. As Möller pointed out, these represent the two extremes of perithecial arrangement in the genus *Cordyceps*. The superficial perithecia on the long linear clavae were all effete, and consequently Möller had to leave the identity of the two forms in doubt, though he inclined to the belief that they were two different species growing from the same larva.

Through the kindness of Dr R. Heim, I have recently been able to examine a specimen from Madagascar, which resembles exactly Möller's figure, except that the long clavae are stouter. It grew on a buried larva, but it was not possible to determine what kind.

In the first form, the perithecial clavae are up to 1.5 cm. high. The stalk is about 0.5 mm. diameter below, attenuated regularly to the apex, terete, sometimes flattened and expanded at the base, red-brown, pruinose. The head develops half-way up the stalk, at first lateral and pulvinate or subglobose, becoming irregularly lobed and encircling the stalk; it is up to 2 mm. diameter, pale brown, dotted with rather large, dark brown, subtranslucent ostiola, which do not project. Thus, the position of the head is similar to that in *Cordyceps unilateralis*, but the colour and texture of the fungus are quite different and resemble those of *C. dipterigena*. The head has a definite cortex, and the perithecia are immersed, perpendicular to the surface, in a peripheral layer. The perithecia are narrow flask-shaped, 0.6 mm. high, 0.25 mm. diameter, the perithecial wall being pale amber, stout, about  $25\mu$  thick. The asci are narrow cylindric, capitate, 4-5 $\mu$  diameter, with linear ascospores in a parallel bundle. The free part-spores are cylindric, becoming slightly narrow oval, 2.5-9  $\times$  1 $\mu$ .

In the second form, the linear clavae are up to 2.5 cm. long, 1 mm. broad, flattened (strap-shaped), twisted, longitudinally furrowed, dark brown, glabrous, sometimes giving off brown, ashy pruinose, terete branches, perpendicular to the main clava, up to 1 cm. long, 0.25 mm. diameter. Towards the distal end, the long clavae are covered with scattered or crowded, superficial perithecia, up to 0.4 mm. high, 0.25 mm. diameter, conico-cylindric or ovate, pale brown, pruinose, thin-walled, apex obtuse. Unfortunately, all the perithecia examined were either effete or immature.

On Möller's specimen, the lateral branches of the linear clavae (the second form) bear, in some instances, perithecial heads of the first form. In the Madagascar specimen, the lateral branches of the linear clavae are conidial, the conidial stage being a *Hirsutella*. The *Hirsutella* phialides are flask-shaped,  $9-11\mu$  high,  $2\mu$  diameter below, attenuated into a stout sterigma. The conidial cluster is limoniform,  $3 \times 1.5\mu$ , and the individual conidia are cymbiform,  $2.5 \times 0.75\mu$ . These dimensions are smaller than is usual in *Hirsutella*, and it is probable that they may be abnormal.

Although it is not possible to arrive at a complete solution of this puzzle, it would appear most probable that the superficial perithecia are those of a *Byssostilbe* or other Nectriaceae, parasitic on the *Cordyceps*. In that case, the whole of the specimen, except the superficial perithecia, belongs to one species, the linear clavae being conidial clavae of the *Cordyceps*.

Theissen (*Ann. Myc.* ix (1911), 68) took the long linear clavae to be *Cordyceps ainictos* Möller, and under that name gave a description of a specimen with linear clavae and superficial perithecia, which he had found in Brazil. But the only identifiable *Cordyceps* which Möller had was the form with pulvinate lateral heads, and it is clear that that form must take Möller's name. Theissen's specimen was not the same species.

*Cordyceps corallomyces* Möller is probably the same as *C. ainictos*. Möller figured a head with strongly projecting perithecia, but he stated that the latter were not superficial, but covered by a definite continuous cortex. In the type specimen, the lateral heads resemble those of *C. dipterigena*, and it is probable that the one figured by Möller is an extreme variation, parallel to that which occurs in the latter species (*Trans. Brit. Mycol. Soc.* x (1924), Pl. I, fig. 6). Against that supposition is the fact that Möller described *C. corallomyces* as red, and it is bright red in his coloured figure in the Berlin Herbarium.

#### 78. *CORDYCEPS LUNTI* Giard

In Saccardo, *Sylloge Fungorum*, xiv (1899), 662, *Cordyceps Lunti* Giard is included, with references to *Bull. Soc. Entom. France* (1895) and *Revue Mycologique* (1899), p. 11. The fungus was said to have occurred on an elaterid larva in France.

The second reference is to a translation, by Ferry, of Massee's *Revision of the genus Cordyceps* in *Ann. Bot.* ix (1895). Ferry added to Massee's paper an appendix which included species described by Quélet and Giard subsequent to its preparation. Among the latter is *Cordyceps Lunti* Giard, for which Ferry did not give any locality.

On referring to Giard's original description, however (*Bull. Soc. Entom. France*, lxiv (1895), p. clxxxi), it is found that the name is

*Cordyceps Hunti*, and that the fungus was from Trinidad. It had been collected by W. Hunt, and sent to Giard by J. H. Hart. Saccardo evidently took his description from Ferry's paper. Similarly, all references in the *Sylloge Fungorum* to Massee's paper are to Ferry's translation in the *Revue Mycologique* (1899), instead of to the *Annals of Botany* (1895), and even in the *Index Iconum*, vol. xix, Massee's figures are cited from the copies in the *Revue Mycologique*.

Giard stated that the clavae and the mycelium which covered the larva were orange-red. Two clavae were present, one almost 5 cm. long, and the other, 3.5 cm. long, regularly thickened upwards, with a conical apex. The stalk was up to 2 cm. long and 1.5 mm. diameter, while the thickest part of the clava was 2.5 mm. diameter. The two clavae had coalesced for a length of 4-5 mm. The perithecia were irregularly scattered, more abundant on one side than on the other, and absent from a small area at the apex, which was not otherwise clearly defined from the remainder of the clava. Apparently the perithecia were immersed, as Giard stated that they formed minute brownish dots on the red clava, presumably referring to the ostiola. Ascii and spores were not recorded.

The description agrees with *Cordyceps martialis* Speg. (*C. submilitaris* P. Henn.). *C. Hunti* should be regarded as another synonym of *C. martialis*.

*Cordyceps Pittieri* Bomm. & Rouss. (*Bull. Soc. Bot. Belge* (1896), p. 160) was described from a specimen on a beetle larva in wood from Costa Rica. The description would fit *C. martialis*, as far as it goes, but the colour could not be stated, as the specimen had been preserved for a long time in alcohol.

#### 79. *CORDYCEPS MELOLONTHAE* (Tul.) Sacc.

In 1824, Jacob Cist contributed a paper, "Notice of the Melolontha or May Bug," to *Silliman's American Journal of Science and Arts*, Ser. 1, viii, 269. In it he mentioned the occurrence, on the larvae of the beetle, of a fungus which sometimes was three inches high. No mycological details were given, and all the information about it is embodied in the first paragraph of Cooke's account of *Cordyceps Melolonthae*. His specimens were North American.

Cist gave three figures. One of them shows two clavae, about one inch high, clavate above, arising from the larva. The other two show single, terete, cylindric clavae, three to four inches long, fimbriate at the apex. It is evident that, if these were *Cordyceps* clavae, they were quite immature.

In *Selecta Fungorum Carpologia*, the Tulasnes named Cist's fungus, *Torrubia Melolonthae*. They had no specimens, but based their name on Cist's figures.

Previously, in 1769, Fougeroux de Bondaroy had described similar fungi on cockchafer larvae from the West Indies. His figures show cylindric clavae which are, in some, slightly inflated at the apex, as though developing an ovoid head. Three of Fougeroux de Bondaroy's figures were reproduced by Cooke (*Vegetable Wasps*, etc., p. 97, text-figs. 20-2).

The Tulasnes referred Fougeroux de Bondaroy's figures to Cist's fungus, *Torrubia Melolonthae*. As, however, they had not examined specimens of either fungus, and both those figured would appear to have been immature, it is quite possible that they are different species. In that case, the name would belong to the North American species.

As no description of *Cordyceps Melolonthae* was possible, and Cist's figures do not represent a mature *Cordyceps*, the name was practically *nomen nudum*. But specimens which corresponded with Cist's figures were apparently frequently collected in North America. It was a common parasite on "White Grub," i.e. the larva of a cockchafer, but was not known in the mature state.

Meanwhile, a *Cordyceps* which was occasionally found on "White Grubs" in North America was referred to *C. herculea* (Schw.) Sacc. It was described and figured under that name by Hard in *Mushrooms, edible and otherwise* (1908), and by Seaver in *The Hypocreales of North America* (1912), the figures in the latter being drawn from a photograph. In Herb. Kew., there is a copy of a similar photograph of an American specimen from W. C. Sturgis.

Lloyd, however, in *Letter 47*, November, 1913, p. 16, note 98, stated that he had examined the type specimen of *Cordyceps herculea* (Schw.) Sacc., and found that it was *Cauloglossum transversarium*. He claimed that the "White Grub" fungus was *Cordyceps insignis* Cke. & Rav. Subsequently (*Mycol. Notes*, No. 39, December, 1915, p. 530, fig. 722), Lloyd adopted the name *Cordyceps Melolonthae*, with *C. insignis* as a synonym, for the American "White Grub" *Cordyceps*.

Hard's photograph of "*Cordyceps herculea*" shows a specimen about 6.5 cm. high, with a stout, cylindric stalk, 2.75 cm. high and 1 cm. diameter, and a broader cylindric head, 4 cm. high, 1.8 cm. diameter, rounded above with a small central knob. The perithecia are apparently immersed, and the lower edge of the head is somewhat irregular, but does not show a re-entrant V. Hard states, "The plant is quite large, clavate in form, the head oblong, round, slightly tapering upwards, with a decided protuberance at the apex.... The head is light yellow."

Seaver's figure (*op. cit.* Pl. 53, fig. 6) shows two clavae developing from one larva. The larger is 5.5 cm. high, with a stalk 8 mm. diameter, and the other, 4.5 cm. high, with a stalk 5 mm. diameter. In both, the fertile part of the clava consists of two longitudinally oval, thickened areas, one on each side of the clava, partly in contact.

Presumably these areas would have extended over the clava until they fused into a continuous head. Seaver described the fungus as "head enlarged and more than 1 cm. thick, with the fertile portion often interrupted, leaving bare patches and in the specimens examined terminated by a short obtuse apex; fertile portion roughened by the slightly prominent necks of the perithecia." From the figures, the obtuse apex is sterile.

Sturgis's photograph is similar to Seaver's figure, but the lateral fertile areas are less developed. Sturgis stated that the colour was livid yellow, and that the part-spores measured  $12.8 \times 2.2 \mu$ .

In a specimen in Herb. British Museum, from "Santa Fe de Bogota," the head is developing from three longitudinal areas, which have not completely fused.

In specimens in Herb. Kew., from South America, several clavae arise close together near the head of the larva. These are all small, the largest being 2.4 cm. high, with a cylindrical head, 14 mm. long, 3 mm. diameter. The whole of the head is fertile, except for a V-shaped groove at the base on each side. One of these specimens, *ex* Herb. Currey, is marked "*Cordyceps* on a larva which destroys the cotton crop in S. America," and was referred by Massee to *Cordyceps sobolifera*.

The most peculiar feature of *C. Melolonthae* is the development of the head from two or more separate areas near the apex of the clava. The perithecia are not embedded in the original clava, but in a superposed thickness of tissue which resembles a parasitic *Hypocreæ*. These areas extend laterally until they ultimately coalesce. The appearance of the head will therefore depend upon the stage of development reached when the specimen is collected. But when the perithecial tissue has become continuous, there is usually a groove, with a V-shaped opening at the base, down one or both sides of the head.

It is to be noted that this development of the head from two or more lateral areas is similar to that of *Cordyceps Volkiana* Möller, found on lamellicorn larvae in Brazil. The clavae of Möller's specimens are more irregular, and in the most regular one the stalk bifurcates above and each branch bears a separate head, but it must be remembered that these clavae were developed under damp conditions, "in eine feucht gehaltene Schale," in the laboratory, and are therefore most probably abnormal. It would only require a bifurcation of the stalk of *C. Melolonthae* to produce *C. Volkiana*.



Fig. 1. *Cordyceps Melolonthae*, from Santa Fe de Bogota.  $\times 1\frac{1}{2}$ .

*C. Cusu* was described by Patouillard from specimens collected by Lagerheim in Ecuador. The specimens were immature. In Herb. Berlin, there are similar specimens from Peru, to which is attached the native name "El Cusso ó Cuzo." The latter were assigned by Hennings to *C. Melolonthae*, and it is probable that they are that species.

As already noted, Lloyd referred *C. insignis* Cke. & Rav. to *C. Melolonthae*. Ravenel sent *C. insignis* to Cooke at Kew, with a note stating that he had found only one specimen, which he had divided into two, forwarding half the fungus and the whole of the large larva. In accordance with that, the other half of that specimen is now in Herb. British Museum, *ex* Herb. Ravenel. But the sheet in Herb. Kew. bears two specimens, and it is evident from Cooke's description that he had two specimens when he described it.

Ravenel's note accompanying the specimens in Herb. Kew. is, "I found but a single example of this and have divided the stipe and capitulum, retaining half. I send the whole of the large larva. The colour is pretty well preserved. I have seen several insect *Cordyceps* here, but this differs from anything I have seen. On dead larva buried in the ground. Seabord of S.C., April 1881. H. W. Ravenel." It is to be regretted that Ravenel did not record what the colour was when fresh, as Cooke did not publish a description until two years later.

On the half specimen in Herb. British Museum, Ravenel's label, as far as it is decipherable, is "*Cordyceps insignis* Cke. and Rav., on dead larva buried in the ground, near . . . ditch, St John's, . . ., S.C., H. W. R."

The sheet in Herb. Kew. contains the half specimen of the fungus, an unattached larva, straight and cylindric, about 2 cm. long and 8 mm. diameter, which is probably the one referred to by Ravenel, and another specimen of the *Cordyceps* with the larva attached. Cooke drew his figure of the fungus from the half specimen, which may be taken as the type. His description covers both specimens.

The half specimen has an obovate or pyriform head, broadest above, about 11 mm. high and 8 mm. broad at its widest part, slightly rough with the apices of the perithecia. The head descends farther down the stalk on one side than on the other and has a median V-shaped groove in its lower edge, so that it may be described as bilobed at its junction with the stalk. The half in Herb. British Museum, which of course shows the other face of the head, is similar. The stalk is about 2 cm. long and 3 mm. broad, and divides at its base into cords of mycelium which become narrow flattened ribbons.

The unattached larva is completely covered by a yellowish film of mycelium, and no segments are evident, nor is the head visible.

The second specimen is remarkably different in appearance. Its

head is irregularly subglobose, or laterally oval, about 1 cm. high and 2 cm. diameter. The stalk is almost wanting, the head being attached to the larva by a twisted stalk-like mass of flattened strands of mycelium. The larva is about 3 cm. long and 1 cm. diameter, but part of the hinder end has been cut off; it is slightly curved, and, like the other specimen, it is covered with a uniform sheet of mycelium which hides the dividing lines of the segments and the head. The strands of mycelium which unite the *Cordyceps* to the larva arise round the head from the sheet of mycelium. On laying bare the anterior end of the larva, it was determined that it was probably a beetle larva, but not a cockchafer.

The two specimens are the same species. The perithecia are wholly immersed, and in section the ostiola barely project. The perithecia are narrow flask-shaped, 0.7 mm. high, 0.25 mm. diameter, now reddish brown above and brownish yellow below. The neck of the perithecium is about 0.1 mm. diameter, but it expands above and becomes about 0.25 mm. diameter with a convex apex. The *Cordyceps* head has a continuous cortex which is composed of the fused apices of the perithecia with very little intermediate tissue. Consequently, it appears in section as composed of agglutinated parallel hyphae, more or less perpendicular to the surface. The part-spores are cylindric with rounded ends,  $4-9 \times 1-1.5 \mu$ . The context of the head is white or yellowish white.

Cooke's figure in *Vegetable Wasps, etc.*, Pl. I, fig. 3, shows the lower edge of the head straight, and in that respect is incorrect. It also shows a solid stalk arising from the larva, which is not in agreement with the specimens. Cooke evidently drew his figure of the fungus from the half specimen, and the larva from the other specimen. His figure shows the segments of the larva, which on the specimen are hidden by mycelium, and a series of triangular processes on the under side. The only justification for these apparent legs is a number of scale-like fragments of wood, about 2 mm. long and 0.5 mm. broad, which are loosely attached to the larva and to one another by fine yellow hyphae. As these fragments occur on both specimens, it may be suggested that the larva is one which surrounds itself with fragments of wood before pupation. When these fragments are cleared away, the larva appears as a uniform mummy without any indication of legs, segments, etc.

*Cordyceps insignis* is not *C. Melolonthae*. In cockchafer larvae attacked by a *Cordyceps*, the fungus arises in one or more stout clavae, generally, though not always, just behind the head. The larva is usually not covered, or only slightly covered by mycelium, and the segments, legs, and horny parts of the head are plainly visible. In *C. insignis*, the larva is completely hidden by mycelium and is attached to the *Cordyceps* by strands of mycelium.

Lloyd was probably influenced in his decision by the presence of a V-shaped groove at the base of the head on either side. But that is the only resemblance. *C. insignis* has a continuous cortex and its perithecia are embedded in the tissue of the head. *C. Melolonthae* is of the intermediate type (*Trans. Brit. Mycol. Soc.* xviii (1933), 51); there is no definite cortex, the tissue between the perithecia is loose and friable, and in section the perithecia appear to be seated on a central core.

Further, the perithecia in a South American specimen of *C. Melolonthae* were ovoid or conoid, 0.25–0.3 mm. high, 0.12–0.16 mm. diameter, less than half the size of the perithecia of *C. insignis*.

Cooke described *C. insignis* as purple. If that is correct, the two species differ in colour.

*C. Melolonthae* appears to be confined to the Western Hemisphere. There is a record of it for Australia by Oliff, which, as Lloyd remarked, appears to be based on "very uncertain material." In the Eastern Hemisphere, the corresponding *Cordyceps* on cockchafer larvae is *C. Barnesii* Thw., which has a much longer, narrower stalk and a smaller head, with a conical sterile apex which may bear the conidial stage, a *Stilbella*. *Cordyceps Barnesii* shows affinity with *C. Melolonthae* in that the fertile portion of the head looks like an extra layer wrapped round the stalk, and it is sometimes grooved, or has a V-shaped opening, on one side. *C. atrobrunnea* Penz. & Sacc., said to be on a Lepidopterous larva, and *C. Fleischeri* Penz. & Sacc., both from Java, appear from the figures and descriptions to be *C. Barnesii*, while *C. obtusa* Penz. & Sacc., also from Java, on beetle larvae, differs from *C. Barnesii* in having the head continuous over the apex.

I am indebted to Mr E. H. Ellis for the photograph of *C. Melolonthae*.

#### 80. *CORDYCEPS HUMBERTI* Robin

In *Monographie des Guêpes Sociales* (1853–8), H. Saussure figured (Pl. V, fig. 9) a *Cordyceps* on *Vespa cincta* from Senegal, which had been named *Cordyceps Humberti* by Robin. He gave a brief account of the fungus, but apparently Robin did not publish a formal description.

Tulasne (*Sel. Fung. Carp.* III (1865), 18) referred the fungus to *Torrubia*, as *T. Humberti*, and gave a description, probably drawn up from Saussure's figure, which is that entered in Saccardo, *Sylloge Fungorum*, II (1883), 576.

The insect bore two perithecial clavae, one from the base of the wings on each side, and several longer and more slender clavae from the sutures of the abdomen. The heads of the perithecial clavae were oval, and rough with projecting ostiola. Cooke's reproduction of the figure omits the details over the surface of the head, merely giving the outline. Two of the slender clavae from the abdomen had minute oval

tips, which were regarded as immature perithecial heads. Gray, as cited by Cooke, stated that these tips were "apparently trifoliated," but in the figure they are simply oval or lanceolate. This suggests that Gray may have seen another figure.

Saussure also gave an illustration (Pl. XI, fig. 5) of another fungus on *Polistes americana*. This fungus had been previously recorded by Felton in 1765 on the same insect (*Phil. Trans.* LIV, 54, Pl. 6). But Felton regarded the fungus as part of the wasp, which he named *Vespa crinita*. Cooke (*Vegetable Wasps*, etc.) named the fungus *Isaria Saussurei*, and it now stands as *Hirsutella Saussurei* (Cke.) Speare.

Tulasne noted that *H. Saussurei* appeared to be related to *Cordyceps Humberti* rather than to *C. sphecocephala*.

I have examined a specimen of *C. Humberti*, on a Hymenopteron, from Sarawak, collected by the Oxford University Expedition to that country in 1932. There were two clavae from the thorax, one from the points of insertion of the wings on each side. One of these was broken. The other was dark brown, 7 mm. long, with an oval swelling, 1 mm. long, 0.4 mm. diameter, about half way up. The stem was slightly thicker below the swelling than above, the upper part being hair-like, tapering to the apex. The swelling is the head, which is not terminal, but not lateral as in *Ophiocordyceps unilateralis*. The head is rough with strongly projecting ostiola, the latter being dark amber, subtranslucent, flask-shaped with a truncate apex, projecting up to  $275\mu$ , and up to  $120\mu$  diameter at the base. The head contained only a few scattered perithecia, and one isolated peritheciatum occurred on the stalk below the head. The asci are  $130\mu$  long,  $10\mu$  diameter, capitate, fusoid or narrow-clavate, the spores in a parallel bundle, but the individual spores not reaching both ends of the ascus. The spores are  $75\mu$  long,  $2.5\mu$  diameter, narrow-fusoid, septate at intervals of 6 to  $16\mu$ , not dividing into part-spores. The fungus is an *Ophiocordyceps*.

Three dark brown, hair-like clavae arose from the last suture but one of the abdomen. These were *Hirsutella Saussurei*.

One frequently finds a minute apical swelling on the clava of *H. Saussurei*. These may be oval or conical, and are sometimes constricted about half-way up, so that in longitudinal section they would appear trifoliate. But they are not represented so in Saussure's figure of *Cordyceps Humberti*. I have always found these tips sterile. It is doubtful whether they are immature perithecial heads as the latter would appear to be always formed in the middle of the clava. In Saussure's specimen the apices of the perithecial clavae had probably been broken off.

*Cordyceps myosuroides* P. Henn., described from a specimen said to be on an Ichneumon from Brazil, is the same species. The host insect is a wasp. Of the two perithecial clavae on the type specimen, one is

immature, and the head is developing some distance below the tip, leaving a long thin apex, while the other is mature, with apparently a terminal head, but examination shows that the upper part of the clava has been broken off. The head is rough with strongly projecting perithecia, which Hennings described as two-thirds free.

*Cordyceps goniophora* Speg. appears, from the description, to be another synonym of *C. Humberti*. It was described by Spegazzini from a specimen on *Mutilla* sp. The clavae were said to be brownish black, setiform, rigid, subhorny, 5–20 mm. long, 0.1–0.3 mm. diameter, generally with an obovate or obclavate swelling, 1 mm. long, 0.5 mm. diameter, about the middle. The clavae were immature and did not bear perithecia. Spegazzini regarded the swellings on the clavae as old heads which had emitted new growths from their apices. The position of the swellings, however, is normal for the heads of *Cordyceps Humberti*, and there does not appear to be any doubt that he had an immature example of that species.

*C. sphecocephala* (Kl.) Cooke, the best known *Cordyceps* on Hymenoptera, has immersed perithecia, ascospores which divide into part-spores, and a *Hymenostilbe* conidial stage. *Cordyceps Humberti* has strongly projecting perithecia, ascospores which do not divide into part-spores, and a *Hirsutella* conidial stage. The synonymy of the latter, as far as has been ascertained at present, is as follows:

*Ophiocordyceps Humberti* (Robin) Petch, comb.nov.; *Cordyceps Humberti* Robin in Saussure, *Mon. Guêpes Soc.* (1853–8), pp. clxiv and 39, Pl. V, fig. 9; *Torrubia Humberti* (Robin) Tul., *Sel. Fung. Carp.* III (1865), 18; *Cordyceps goniophora* Speg. in *Bol. Acad. Nac. Cienc. en Córdoba (República Argentina)*, XI (1889), 537; *Cordyceps myosuroides* P. Henn. in *Hedwigia*, XL (1902), 169. Conidial stage, *Hirsutella Saussurei* (Cke.) Speare in *Mycologia*, XII (1920), 69; *Isaria Saussurei* Cooke, *Vegetable Wasps*, etc. (1892), p. 53; *Isaria crinita*, Lloyd, *Mycol. Notes*, No. 54 (June, 1918), p. 778, fig. 1173.

### 81. *CORDYCEPS PUIGGARII* Speg.

In *Fungi Argentini*, Pugillus IV, No. 207, Spegazzini recorded *Cordyceps sphecocephala* on *Polybia fasciata*, and gave a re-description which was included in Saccardo, *Sylloge Fungorum*, II (1883), 568. Subsequently Spegazzini decided that his fungus was not *Cordyceps sphecocephala*, and in *Fungi Puiggariani*, Pugillus I (1889), 157, he described it as *C. Puiggarii* n.sp. He stated that the head was attenuated into a rather long, acute, conical, sterile apex. That, however, is not uncommon in *C. sphecocephala*, and the other details given by Spegazzini do not show any differences from that species. Its perithecia were said to be "immersa, vix prominula"; hence it cannot be referred to *C. Humberti*. The name *Cordyceps Puiggarii* Speg. was duly entered in Saccardo, *Sylloge Fungorum*, IX (1891), 1000.

In 1919 (*Bol. Acad. Nac. Cienc. Cordoba*, xxiii, extr. p. 116), Spegazzini described another species as *Cordyceps Puiggari*. This was on a beetle, *Lystronychus* sp., and from the description it would appear to be *Cordyceps curculionum* (Tul.) Sacc.

## 82. CORDYCEPS on Orthoptera

The species of *Cordyceps* recorded on Orthoptera include *C. locustiphila* P. Henn., from Brazil, *C. amazonica* P. Henn., from Brazil, and *C. Uleana* P. Henn., from Peru, all described in 1904, and *C. stiphrodes* Syd. and *C. ctenocephala* Syd., from New Guinea, described in 1922. The last-named was said to be on a Cicada, but it would appear to be on a Locustid.

*C. locustiphila* differs from *C. amazonica* in the shape of the head. In the type of the former, the clavae are curved from beneath the insect and terminate in laterally compressed, clavate heads, about 8 mm. long, 2 mm. diameter. In *C. amazonica*, the clavae are short and erect, and the heads are ovoid, about 4 mm. high, 3.5 mm. diameter, contracted abruptly into the stalk. In both, the heads are minutely rough with red-brown, slightly projecting ostiola, with a pale brown, detersive pruina between the ostiola, and the perithecia are immersed. The two agree in all essential details, and *C. amazonica* must be regarded as a synonym of *C. locustiphila*. I have a specimen from Trinidad, on a mole cricket, in which the head is globose.

Judging from the figure and description, *C. stiphrodes* Syd. is *C. locustiphila*.

The type of *C. Uleana* has clavae with a short stout stalk and a globose head with strongly projecting perithecia. I have been able to examine two other specimens of this species from Madagascar, one mature and the other immature, on Phasmids. According to the collector's note, the colour when fresh was pale yellow. The immature clavae are now white, up to 4 mm. high, usually simple, sometimes concrecent at the base, with a stalk up to 0.5 mm. diameter below, usually expanding upwards and terminating in a globose or ovoid head, up to 1 mm. diameter, dotted with minute yellow-brown points which are the initials of the perithecia. In the mature specimen, the heads are up to 1.5 mm. diameter, strongly echinulate, and consist of a group of strongly projecting perithecia, with mycelial tissue between their bases. The perithecia are now dark amber, tomentose below, conoid with an acute apex, up to 0.4 mm. high, 0.25 mm. diameter, projecting three-quarters of their height. The asci are cylindric, capitate,  $4\mu$  diameter, and the ascospores linear,  $1\mu$  diameter, in a parallel bundle. The part-spores are cylindric,  $3-9 \times 1\mu$ . *C. Uleana* resembles the form of *C. tuberculata* (*C. Sphingum*) which Curtis named *C. isariooides*.

In Herb. Kew., there is a specimen of *C. Uleana*, collected by Traill in Brazil in 1874. It is included in the cover of *C. Sphingum*, and is the basis of Cooke's statement that *C. Sphingum* "is said to occur also on *Orthoptera*," and Massee's later record of that species on a small Orthopterous insect. The insect bears slender clavae, each bearing superficial, scattered or clustered perithecia. A similar specimen, now in Herb. Berlin, was collected by Tessmann in Peru, and I have examined another, with immature clavae only, from British Guiana (coll. E. B. Martyn).

*C. ctenocephala* Syd., judging from the figure and description, is *C. Uleana*.

Lloyd (*Mycol. Notes*, No. 62 (1920), p. 913, fig. 1622) suggested that *C. Joaquiensis* P. Henn., recorded by Hennings with a query as on a Coleopterous larva, was on a mole cricket, as he had received specimens on mole crickets which resembled Hennings's figure, and the host in the figure appeared to him to be a mole cricket. But the figure shows the host completely enveloped by mycelium, and its nature must remain uncertain, until the type specimen is re-examined.

### 83. *CORDYCEPS SOBOLIFERA* (Hill) Sacc.

The fungus which grows on Cicada nymphs, and is now known as *Cordyceps sobolifera*, has been the subject of numerous articles, the relevant data from which were republished by Cooke in his *Vegetable Wasps and Plant Worms*. It was named *Clavaria sobolifera* by Hill, in *An account of the insect called the Vegetable Fly* by W. Watson in *Phil. Trans. Roy. Soc.* LIII (1763), 271-4, with a figure. Hill had specimens from Martinique, and Watson from Dominica. A few years later, Fougeroux de Bondaroy contributed a paper, *Sur les insectes sur lesquels on trouve des plantes*, to *Hist. l'Acad. Roy. des Sciences, Paris*, année 1769 (1772), pp. 467-76, Pls. 4, 5, in which he included the Cicada fungus without stating the origin of his specimens, though they were no doubt from the West Indies. Cooke (*op. cit.*) reproduced three figures from Fougeroux de Bondaroy, but he turned one of them (Cooke, fig. 45) through 90°.

*Cordyceps sobolifera* owes its name to the fact that Hill's specimen bore lateral, more or less oval outgrowths (soboles) about the middle of the stem. These outgrowths are conidial, and are apparently easily detached, so that the mature *Cordyceps* may not be soboliferous. The early figures show usually a lobed head, or more rarely a simple cylindric head, with or without soboles on the stem.

The conidial stage of *Cordyceps sobolifera*, *Isaria Cicadae* Miq., usually has a much branched and lobed head, the lobes being powdery with conidia, but it may have a head of few lobes, in which the lobes are even and compact, appearing at first glance to be perithecial clavae.

Judging from the figures, Watson's specimen, and those figured by Fougeroux de Bondaroy, were conidial clavae. Fig. 7, Plate 4, of the latter writer, which shows a long cylindrical head, may represent a perithecial clava, but he did not state that it differed in texture from the others.

The first formal description of *Cordyceps sobolifera* was published by Berkeley in 1843 in *Hooker's London Journal of Botany*, II, 207, under the name *Sphaeria sobolifera*. He described it as "carnosa, pallide fusca; capitulo subgloboso, stipite aequalitereti proliifero." Berkeley did not cite any type specimen, but stated that there were several specimens in the herbarium of the British Museum. There are two old specimens now in Herb. British Museum, marked "Vegitans, W. I.," without date. In both, the stalk is simple, without processes. In one, the head is elongated oval, 7 mm. long and 4 mm. diameter, and the stalk about 2 cm. long, 2 mm. diameter in the middle, attenuated above and below. The other is apparently immature, and has a cylindrical head, 6 mm. long, 2 mm. diameter, and a stalk about 3 cm. long, 2 mm. diameter in the middle, not noticeably attenuated above and below. The head is sharply defined from the stalk, and terminates in an even line round the latter.

In all the undamaged specimens of *Cordyceps sobolifera* which I have seen, the head is oval, or cylindric, or subglobose, and terminates evenly below, while the stalk is cylindric and does not bear soboles.

A specimen from Madagascar, in Herb. Berlin (*C. Voeltzkowii* P. Henn.), is accompanied by a drawing which shows soboles on the stem, but there are none on the specimen now. On the other hand, a Ceylon specimen did not bear any soboles when collected. The name, *C. sobolifera*, is unfortunate, as it would appear that the perithecial clava either does not bear soboles, or if it does they are not persistent.

The Tulasnes included *C. sobolifera* (as *Torrubia*) in *Selecta Fungorum Carpologia*, III (1865). They stated that the head was ovato-oblong or linguaeform, with a thick, terete, rigid, erect, glabrous and naked stalk, but sometimes the stalk bore a few short branches, either crowded in the middle, or remote and alternate. It would appear that they deduced the last statement from the literature, as they stated that in the specimens they had from Martinique, the stalks were simple and naked. The soboles are scarcely branches of the stem, but oval bodies loosely attached at their bases.

Fig. 2. *Cordyceps sobolifera*, from Vegitans, W. I.  $\times 1\frac{1}{2}$ .



The Tulasnes gave a figure showing the whole fungus attached to the insect, and, as that specimen was immature, they supplied a drawing of part of an ascus with part-spores from another specimen. Their figure created some difficulty, as it differs in an important feature from the available specimens. It shows, down the head, a longitudinal groove which opens out into a V-shaped gap at the base, whereas on recent specimens the head is uniformly terete and the lower edge is even. The figure, indeed, more closely resembles some specimens of *C. Melolonthae*, in which species the longitudinal groove and V-shaped opening are a consequence of the peculiar mode of development of the head, and it is interesting to note that Cooke (*Vegetable Wasps*, etc., p. 96, footnote) cited the Tulasnes' figure as an illustration of *C. Melolonthae*.

Lloyd pointed out that the specimen from which the Tulasnes' first figure was drawn is still in the Paris herbarium, and, through the courtesy of the officers in charge, I have been permitted to examine it. The specimen agrees with the figure, but it is evident that the groove is accidental and due to pressure or shrinkage in drying. The head is flattened, and one side is grooved as shown in the figure, while on the other side the groove begins at the apex, but does not extend to the base.

The specimen recorded from Ceylon as *C. gracilis*, and figured in *Trans. Brit. Mycol. Soc.* x (1924), Pl. I, fig. 2, is *C. sobolifera*. The record of *C. sobolifera* on cockchafer larvae, in *Fungi of Ceylon*, No. 978, is, as previously noted by Massee, an error, the fungus being *C. Barnesii*. The latter record is the basis of the statement in Saccardo, *Syll. Fung.* II (1883), 569, that *C. sobolifera* occurs on Lamellicorn larvae.

Massee (*Ann. Bot.* IX (1895), 13) recorded *C. sobolifera* on the larva of a beetle, probably one of the Melolonthidae, South America, the specimen having a note on the label, "on a larva which destroys the cotton crop in S. America." This specimen is still in Herb. Kew., but it is not *C. sobolifera*.

As already indicated, *C. Voeltzkowii* P. Henn., from Madagascar, is *C. sobolifera*.

*C. sobolifera* is known, in its perfect stage, from the West Indies,

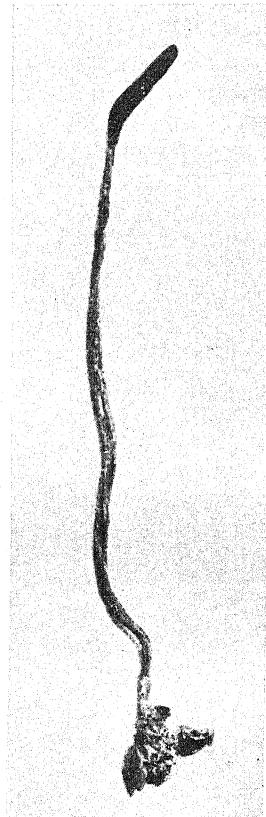


Fig. 3. *Cordyceps sobolifera*, from Madagascar.  $\times \frac{1}{2}$ .

Japan, Ceylon, and Madagascar. The conidial stage is known also from Mexico, China, and New Zealand.

In colour, *C. sobolifera* is at first white with a pinkish tinge, becoming brown. In dried specimens, the stalk is pale brown to rufous brown, and the head red-brown with darker ostiola. In a collector's note on a Madagascar specimen, the fungus is said to be red-brown. The total height in the available specimens varies from 2.5 cm. to 11 cm. The stalk is from 2 cm. to 9.5 cm. long, terete, sometimes equal, sometimes inflated in the middle. A large specimen from Madagascar has a stalk 2.5 mm. diameter below, expanding to 4 mm. in the middle and diminishing to 3 mm. at the apex. The stalk is glabrous and even when fresh, but may become longitudinally furrowed in drying. The head is usually sharply defined from the stalk when fresh, but it may not be so distinct on dried specimens; it may be cylindric, oval, or subglobose, up to 1.8 cm. high and 9 mm. diameter. On large specimens the head is small in comparison with the stalk. The perithecia are immersed, and on a fresh specimen the ostiola were not evident, but on herbarium specimens the head is rough with slightly projecting ostiola, darker than the head. The perithecia are flask-shaped with a rather long neck, 0.4-0.6 mm. high, 0.3 mm. diameter.

In a Ceylon specimen, the asci were 8 $\mu$  diameter and the part-spores cylindric, 4-8  $\times$  2 $\mu$ . Patouillard has noted the breadth of the ascus as 8 $\mu$ , and the length of the part-spores as 7-8 $\mu$ , on a specimen from Madagascar in Herb. Paris. Hennings stated that the ascospores of *C. Voeltzkowii* were 1.5-2 $\mu$  diameter, and Lloyd (*Mycol. Notes*, No. 42 (1916), p. 584) gave the part-spores as 8-12  $\times$  1 $\mu$  in a specimen from the Bahamas.

I am indebted to Mr E. H. Ellis for the photograph of *C. sobolifera* from the West Indies.

#### 84. *CORDYCEPS STENOCORI* Quélét

*Cordyceps Stenocori* was described and figured by Quélét in *Assoc. Franç. pour l'Avanc. d. Sci.* xxiv (1895), 622, Pl. 6, fig. 18. It occurred on a beetle, *Stenocorus mordax* Fab. From the figure and description, it was evidently a conidial form only.

From Quélét's remark, that it appeared to be very near *C. militaris*, one might deduce that it was the form of *Spicaria* (*Isaria*) *farinosa* which occurs on beetles, but the description of the conidia as ellipsoid, 5 $\mu$ , bi- or tri-guttulate, is against that supposition. The figure resembles some forms of *Hirsutella Eleutherorum*, but does not show the seta-like phialides. The conidia are figured as oval, with a well-marked cylindric apiculus. Until the type is re-examined and the conidiophore determined, this species cannot be classified, except indefinitely as *Isaria*.

85. *STEREOCREA COCCOPHILA* Petch, n.sp.

This species occurred on a scale insect on *Eugenia*, at Nuwara Eliya, Ceylon, January 16th, 1927.

The stromata are at first flattened pulvinate, up to 4 mm. diameter, 1.25 mm. high, completely covering the scale. Ultimately they become irregularly tuberculate, up to 7 mm. diameter, with flattened turbinate tubercles, the convex upper surface of which is oval in plan and up to  $2.5 \times 1.5$  mm., or larger by confluence. At first they are red-brown, but become black with a greyish bloom. Internally they are orange-yellow. Alcohol gives a yellow extract, which turns yellow-brown with caustic potash. The context is rather soft and crumbly, and consists of stout, thick-walled hyphae, with deposits between them as in *Myriangium*. In the young pulvinate stroma, there is a well-marked cortical layer of radial parallel cells, and in the centre of the stroma, chains of cells not united laterally. In the older stromata, the cortex is stout and black, but the cells are not radial. The blackening is due to a blackish green deposit between the cells. The cortex breaks up when old, but it is not carbonaceous.

The perithecia are situated in the tubercles, none having been observed in the merely pulvinate stromata. They are irregularly placed, sometimes distant, sometimes crowded, peripheral, usually in a single layer, 0.4 mm. high, 0.25–0.3 mm. diameter, subglobose or ovoid, with a short conical neck. The perithecial wall is yellow, about  $30-40\mu$  thick, composed of parallel slender hyphae. The ostiolas are not evident externally. The perithecia are polyascigerous, the asci being clavate,  $140\mu$  long (including a pedicel about  $40\mu$  long),  $24\mu$  diameter, soon diffluent, eight-spored, the spores being obliquely uniseriate below and biseriate above. The apex of the ascus is not thickened and does not turn blue with iodine. There are no paraphyses. The ascospores are cylindric with rounded ends, hyaline, 3 to 5 septate, not or slightly constricted, minutely warted, with a hyaline mucous coat,  $32-50 \times 10-12\mu$ .

The general appearance and structure of the stroma are those of *Myriangium*. The loculi, however, are ostiolate and polyascigerous.

*Stereocrea coccophila* Petch, n.sp.—Stromatibus immaturis depresso-pulvinatis, usque 4 mm. diam., 1.25 mm. alt., dein irregulariter tuberculatis, tuberculis confertis, depresso-turbinatis, supra convexis; extus primo rufo-brunneis, dein nigris, intus aurantiacis; peritheciis in tuberculis sitis, periphericis, saepius monostichis, confertis vel sparsis, subglobosis vel ovoideis, 0.4 mm. alt., 0.25–0.3 mm. diam., collo conico brevi, omnino immersis, ostiolis non emergentibus, pariete flavo,  $30-40\mu$  crasso, ex hyphis tenuissimis dense parallele dispositis; ascis clavatis,  $140 \times 24\mu$ , mox diffluentibus, octosporis;

sporis cylindraceis, utrinque rotundatis, hyalinis, 3-5 septatis, non vel leniter constrictis, minute granulatis, muco hyalino indutis, 32-50  $\times$  10-12  $\mu$ .

On a scale insect on *Eugenia*, Nuwara Eliya, Ceylon.

86. *ENTOMOPHTHORA APHROPHORAE* Rostrup

*Entomophthora Aphrophorae* was briefly described by Rostrup in 1896 (*Botan. Tidskr.* xx, 128, with figure). It occurred on *Aphrophora spumaria* (= *Philaenus spumarius*), a froghopper, in Denmark. He stated that, when fully developed, it was of a bright orange colour.

Specimens were collected on *Philaenus spumarius* on bramble at Arncliffe Woods, near Whitby, in August, 1930 (F. A. Mason), and at Grassington in September, 1931, but owing to their condition when received or collected they were passed over as *Entomophthora sphaerosperma*. In September, 1933, a specimen on *Philaenus* sp. was received from Fritton Bog, Suffolk, while it was collected in quantity at Aldbrough and Hedon, East Yorks., and in smaller numbers at Lartington and Deepdale, North-West Yorks., and at Dipton Wood near Corbridge. The majority of the specimens occurred on the under side of leaves of *Ranunculus repens*, but it was found also on *Plantago lanceolata*, *Carduus arvensis*, *Juncus*, etc.

The insect is attached to the leaf by fascicles of coarse brownish rhizoids, which are not expanded or lobed at the extremity, from the under surface of the body. The conidiophores form a stroma which appears round the insect and along the back between the wings, and ultimately extends so as to cover the whole insect, except for two parallel, longitudinal, oval areas, one over the middle of each wing. The fully developed stroma is remarkably thick, compact, waxy-looking, viscid, at first yellow or greenish yellow, becoming orange or reddish. Cystidia were not observed. Although the stroma is exceptionally thick, it rapidly shrinks, after maturity, to a very thin translucent film, and specimens in the latter condition could not be identified correctly without a previous knowledge of the fungus.

The conidia are narrow oval, with a convex papilla occupying the whole base and defined by a collar. They are sometimes surrounded by a hyaline mucous coat, thickest at the apex (3  $\mu$ ) and continuous or discontinuous along the sides, but not extending over the base. Their contents are granular, sometimes with a central nuclear body. On dried specimens from Arncliffe Woods (1930), the conidia found measured 20-24  $\times$  6  $\mu$ , and on similar specimens from Grassington (1931) they were 21-30  $\times$  7-9  $\mu$ , while in a spore print obtained from fresh specimens at Hedon in 1933, they were 20-30  $\times$  7-10  $\mu$ , usually about 27  $\times$  8  $\mu$ . Rostrup gave the dimensions as 16-18  $\times$  7-8  $\mu$ . Compared with *Entomophthora sphaerosperma*, the conidia are longer and more regularly oval.

Germination occurs from the middle of one side of the conidium. The secondary conidia are either obpyriform, curved at the apex,  $12-18 \times 7-9 \mu$ , on a slender conidiophore, up to  $60 \mu$  long,  $2 \mu$  diameter at the base, tapering to  $1 \mu$  above, or broadly oval,  $12-20 \times 8-9 \mu$ , apex usually acuminate, on a stout conidiophore,  $9 \mu$  long,  $6 \mu$  diameter.

The resting conidia (azygospores) are spherical, hyaline, thick-walled ( $3 \mu$ ),  $25-33 \mu$  diameter.

*E. Aphrophorae* differs from *E. sphaerosperma* in the consistency of its stroma, in its longer and more oval conidia, and in the shape of the secondary conidia.

#### 87. *EMPUSA MUSCAE* Cohn

This species is usually recorded as occurring on house flies attached to window panes in the autumn. In my experience, it is much more common out-of-doors during the summer months, when it may be found on flies of several kinds, but especially on "dung flies" (*Scatophaga* spp.) on the flower heads of grasses, *Juncus*, *Rumex*, *Senecio*, and *Umbelliferae*. In 1933, I received specimens on dung flies collected in June in Oxfordshire, Staffordshire, and Surrey, while in July, 1931, I saw hundreds of examples, chiefly on dung flies, in East Yorkshire. It is most abundant on marshy ground, especially in wet seasons, but examples may be found at random over the country every year.

The dung flies are not attached to the plant by their probosces, as are the flies on a window pane, but merely clasp the inflorescence with their legs.

One point in which the *Empusa* on the dung flies appeared to differ from *Empusa Muscae* was the presence of a rather broad longitudinal band of conidiophores forming a stroma along each side of the abdomen on the lower surface. This raised doubts about the identity of the species, as, according to all accounts, *E. Muscae* does not form a continuous stroma over the body of the fly. In most species of Entomophthoraceae on flies, the conidiophores first appear along the sutures, and subsequently spread and coalesce, covering the whole of the body, except sometimes the centre of the thorax. In *E. Muscae*, however, the conidiophores remain restricted to the sutures, so that the abdomen is encircled by white rings. But on examining a specimen of *E. Muscae* on a house fly, which had died in the classic manner on a window pane, it was found that it had two narrow longitudinal continuous bands of conidiophores along the under surface of the abdomen. There was therefore no difference between the distribution of the fungus on *Scatophaga* and that on *Musca*, the greater development of the longitudinal bands on the former being probably due to a more humid environment in the open.

While it is correct that the conidiophores of *Empusa Muscae* do not

coalesce over the body of the insect, they do coalesce along its sides or under it.

It is probable that *Empusa Muscae* on *Scatophaga* is what was named by Giard, *Entomophthora Scatophagae*, without description. Giard stated that it resembled *Empusa Muscae*, but differed from that species in its larger yellow conidia. The conidia on *Scatophaga* do appear yellowish in mass on dried specimens, though not when fresh, but they are within the range of dimensions of *Empusa Muscae*. Giard also stated that the dead insect was fixed by its feet and abdomen, from which Guéguen deduced that *Entomophthora Scatophagae* possessed rhizoids, but the deduction does not appear to be warranted. The feet of the insect are entangled in the inflorescence of the plant.

*Entomophthora Syrphi* Giard (*nomen nudum*) would appear to be also *Empusa Muscae* out-of-doors.

I have not seen any record of *Empusa Muscae* except on flies. In August, 1933, Mr F. T. Brooks sent me from Cambridge a capsid bug (*Lygus pabulinus*) which had attracted attention by its enormously distended abdomen. Sent in a tin box, it died in transit and developed typical *E. Muscae*. The primary conidia were the normal shape, and the secondary conidia were the same shape or oval. The specimen, therefore, could not be assigned to *Empusa erupta* Dustan, which was described from *Lygus communis* var. *novascotiensis* in North America.

#### 88. *ASCHERSONIA CAESPITICIA* Syd.

*Aschersonia caespiticia* was described by Sydow in *Engler's Bot. Jahrb.* LIV (1916), 260, from specimens from New Guinea. Through the kindness of Dr Sydow, I have recently received part of the type specimen.

The stromata are up to 3 mm. diameter, pulvinate, covered with ovate or subcylindric processes. The *Aschersonia* pycnidia are situated near the base of the stroma, and are completely immersed, oval in plan, but with the sides convoluted, so that the pycnidia appear labyrinthoid in section. The ostiolum is small, and does not project, and the pycnidium communicates with the exterior through a tube of varying length. The pycnospores are narrow fusoid,  $9-13 \times 1-1.5 \mu$ , rarely  $2 \mu$  broad, and there are no paraphyses. The fungus is on a *Lecanium*.

This is the *Aschersonia* stage of *Hypocrella Amomi* Rac. The projections are the perithecial processes, but in the specimen examined they were solid and immature. The entire fungus agrees with the figure of *H. Amomi*, *Ann. Perad.* VII (1921), Pl. II, fig. 5. In the type specimen of *H. Amomi*, the perithecia and the pycnidia occurred in separate stromata. In the present collection, they are combined in the same stroma, but the perithecial processes are immature.

89. *PATELLINA EPIMYCES* Petch, n.sp.

This species was collected at Peradeniya, Ceylon, in May, 1921, growing on a brown or greyish brown stroma on a froghopper on mango leaves. This stroma, which covers the insect almost or completely, is frequent at Peradeniya, but is generally sterile. It has recently been determined as that of *Hirsutella versicolor*, a species which is usually fertile when found at higher elevations.

The same *Patellina* was collected by Miss E. M. Wakefield in Trinidad in 1921, parasitic on *Hirsutella entomophila* Pat. In the Ceylon specimens, which occur on the even continuous stroma covering the insect, the sporodochia are flat and saucer-shaped, but in the Trinidad specimens, in which they are seated on the very slender clavae of *H. entomophila*, they are obconic.

*Patellina epimyces* Petch, n.sp.—Sporodochiis discoideis, rotundatis vel lobatis, usque 0.5 mm. diam., 0.1 mm. crassis, vel obconicis, usque 0.15 mm. diam., 0.1 mm. alt.; disco aurantiaco-rubro, ceraeo, margine albo pruinoso; extus albis, tomentosis, ex hyphis parallelis supra clavatis, 2.5–4  $\mu$  diam., minute verrucosis, compositis; conidiophoris confertis, ampullaceis, 9  $\mu$  alt. infra 2  $\mu$  diam., ad 0.5  $\mu$  diam. supra attenuatis; conidiis angusto-ovalibus, utrinque acutis, hyalinis, 2–4  $\times$  1–1.5  $\mu$ .

Parasitic on *Hirsutella versicolor* Petch, Peradeniya, Ceylon, and on *H. entomophila* Pat., Trinidad.

90. *HIRSUTELLA ENTOMOPHILA* Pat.

This species which occurs on beetles was described by Patouillard in *Rev. Myc.* 1892, p. 69, as having rigid simple clavae. A number of specimens were collected by Dr C. B. Williams at Mareval, Trinidad, in 1916, and others by Miss E. M. Wakefield at Moruga, River Estate, and elsewhere in the same country in 1921. Some of these are more developed than the specimens described by Patouillard, and are extensively branched.

The clava is up to 1 cm. high. It consists of an erect, rigid, hair-like main stem, about 0.1 mm. diameter at the base, which divides only near the apex, if at all. From this stem, primary lateral branches, about 0.04 mm. diameter, up to a dozen or more, somewhat distant from one another, spread horizontally, and these bear secondary lateral branches, about 0.02 mm. diameter, which extend horizontally and vertically. Branching is always practically at right angles, and the branches are usually straight and rigid, but may be curved at the tips. The fungus thus forms a tree-like structure. Several of these clavae may arise from the body of the beetle, and others from brown strands of mycelium which run from the insect over the surface of the leaf to which it is attached, as far as 2 cm. from the insect.

These dendroid clavæ suggested comparison with *Isaria ramosissima* Zoll. & Mor., found on the elytra of a beetle in Java, and described in *Natuur- en Geneeskundig Archief voor Néerland's-Indie*, 1 (1844), 376. The original description of the latter species is "Subgregaria, basi flavescenti-albida, apicem versus candida, dendroidea ramosissima, ramulis farinaceis. Ad elytra caraborum emortuum inter folia putrida in silvis prope Tjikojja, provinc. Batav. Mense Apr. Clavarioidea est parum fugax; stipes basi radiciformis subgeniculatis sub-solidus; rami apice subfasciculati, fere crisi, in sinubus dilatati."

*Hirsutella entomophila*, in the available specimens, is brown, ashy at the tips, and therefore apparently differs from *Isaria ramosissima* in colour, though it is possible that it may be white at first. The other details of the latter species, as far as they go, do not agree with *Hirsutella entomophila*.

#### 91. *HIRSUTELLA FORMICARUM* Petch, n.sp.

In *Trans. Brit. Mycol. Soc.* x (1924), 35, it was recorded that the conidial stage of *Cordyceps unilateralis* (Tul.) Sacc. occurred on the apex of the perithecial clava and was a *Hirsutella*. That has since been confirmed on specimens from British Guiana, collected by Mr Paul Richards, with the additional fact that the fungus may also produce independent conidial clavæ.

In Mr Richards's specimens, the number of perithecial plates on a clava varies from one to four. If the tip of a clava has been broken off, a plate may bend over the broken end and simulate a terminal hemispherical head; or two plates may occur on opposite sides of the clava, with a similar effect. The perithecial clavæ usually arise from the head of the insect and bear conidiophores towards the apex, but independent conidial clavæ may arise anywhere, from the body, legs, or antennæ. This conidial stage may be known as *Hirsutella formicarum*.

*Hirsutella formicarum* Petch, n.sp.—Clavis linearibus, usque 17 mm. alt., e corpore insecti oriundis, vel apicem stromatis *Cordyceps* formantibus, brunneis, tomentosis, supra cinereis; basibus phialidum ovalibus, 8-11 x 4-6  $\mu$ , in sterigma, 20  $\mu$  alto, basi 1-1.5  $\mu$  diam., sensim attenuatis; conidiis angusto-cymbiformibus, obtusis, 9-11 x 2  $\mu$ , muco coalitis. Status conidiophorus *Ophiocordyceps* *unilateralis*, British Guiana; Ceylon.

92. *HIRSUTELLA RADIATA* Petch, n.sp.

Several examples of this species were collected by Dr C. B. Williams at Essequibo, British Guiana, September 11th, 1916. It occurred on a small fly, which was attached to a leaf by a small pad of brown mycelium.

The fungus arises from the thorax of the insect as a slender rigid column, 1-2 mm. high, 0.1 mm. diameter. From the apex of this basal column, rigid branches, up to 1 cm. long, 35-45  $\mu$  diameter, to the number of three or four, spread out horizontally, curving downwards at the tip. These branches may bear, near the distal end, a pair of opposite branches which similarly curve downwards. In some specimens, the basal column is continued upwards as a central stem for a length of about 7 mm., or this may curve over and appear as

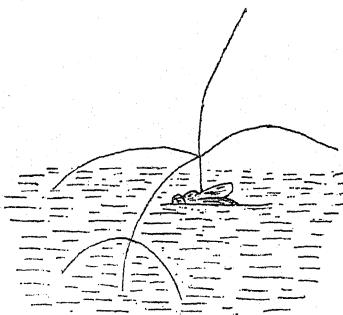


Fig. 4. *Hirsutella radiata*.  $\times 6$ .

another branch. The colour of the whole fungus is dark brown or rufous brown, cinereous towards the tips, with a matt surface. The body of the host fly is only about 2 mm. long.

The phialides have a conical base,  $5-8 \times 3-4 \mu$ , merging into a stout sterigma,  $9-14 \mu$  long, or a cylindrical base,  $6-18 \times 2 \mu$ , with a sterigma  $6 \mu$  long. In many of the latter, the base and sterigma together form a uniformly conical whole and can be differentiated only by staining. The spore cluster is oval,  $9-11 \times 6-7 \mu$ , and the individual conidia are cymbiform,  $6-9 \times 2-2.5 \mu$ , or oval,  $7-8 \times 3-4 \mu$ .

*Hirsutella radiata* Petch, n.sp.—Clavis erectis, rigidis, 1-2 mm. alt., 0.1 mm. diam., apice ramos horizontales ferentibus, truncatis, vel in flagellum usque 7 mm. alt. productis; ramis rigidis usque 1 cm. longis, 35-45  $\mu$  diam., apicem versus decurvis et saepe ramulos duos oppositos ferentibus; fusco-brunneis vel rufo-brunneis, apicibus cinereis; phialidibus basi conico,  $5-8 \times 3-4 \mu$ , in sterigma, 9-14  $\mu$

longum, attenuato, vel basi cylindraceo,  $6-18 \times 2 \mu$ , sterigmate  $6 \mu$  longo; conidiis cymbiformibus,  $6-9 \times 2-2.5 \mu$ , vel ovalibus,  $7-8 \times 3-4 \mu$ .

On flies, British Guiana.

93. *BLASTOTRICHUM ARANEARUM* Petch, n.sp.

The genus *Blastotrichum* was established by Corda in *Icones Fungorum*, II (1838), 10, for a species, *Blastotrichum confervoides*, found on living and dead parts of a hydrophilous *Euphorbia*. From the submerged parts of the plant it spread through the water in lax woolly masses, but round the stem at water level it produced aerial tufts of crowded conidiophores.

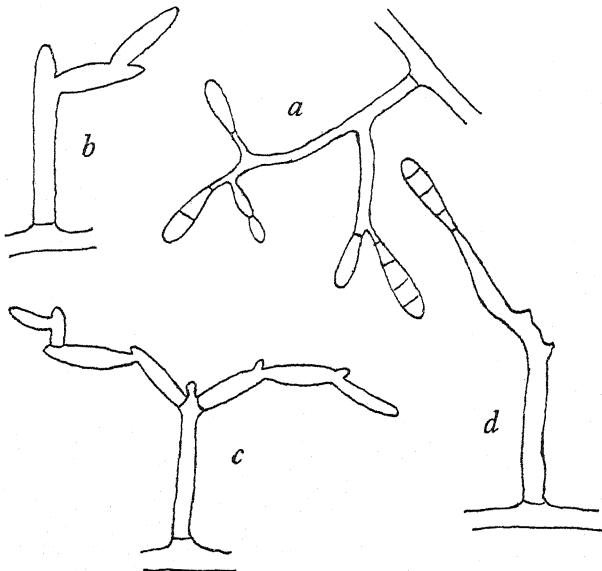


Fig. 5. *Blastotrichum Aranearum*. a, lax conidiophore from the body of the spider; b, c, d, rigid conidiophores from the legs. All  $\times 1000$ .

A species referable to this genus has been found in Ceylon on spiders. In one specimen, in which the spider is concealed beneath a sheet of silk, the mycelium forms a loosely interwoven mat on the silk sheet, with small, waxy, pale amber, translucent masses of conidia; the conidiophores of this specimen are somewhat lax and decumbent, and have no septa, except the basal septum which cuts off the conidiophore from the hypha (Fig. 5a).

In another specimen, in which the spider was attached to a living leaf, without any cover, the conidiophores on the body of the insect are similar, but, in addition, conidiophores are present in rows along the legs of the spider, and these conidiophores are erect and rigid,

either sympodial (Figs. 5 *b*, *d*) or cymosely branched. Some septa are present in the branched conidiophores, especially when the conidiophore bifurcates, a septum being then produced in each branch near its base (Fig. 5 *c*).

*Blastotrichum Aranearium* Petch, n.sp.—*Hyphis* crassis,  $2.5-3\mu$  diam., insectum stromate laxo albo obducentibus; conidiophoris crassis,  $2-3\mu$  diam., intus granulosis, saepius non septatis, simplicibus vel cymose vel sympodialiter ramosis; conidiis hyalinis, fusoideis vel clavatis, utrinque rotundatis,  $1-3$  septatis,  $16-24 \times 3-3.5\mu$ .

On spiders, Nuwara Eliya, Ceylon.

94. *VERTICILLIUM FULIGINOSUM* Petch, n.sp.

This species was collected by Dr C. B. Williams on a leafhopper on sugar cane at Marienburg, Surinam, May 19th, 1916, and at Bocas, Panama, March 9th, 1917.

The mycelium on the insect is at first white, then fuliginous, and spreads from the insect over the leaf in a blackish film. The hyphae are stout,  $5-10\mu$  diameter, regular, pale fuscous, with black zones at the septa, which shade off on either side or sometimes extend over a whole segment. This peculiar coloration of the hyphae is very striking. The conidiophores are up to  $500\mu$  high,  $7\mu$  diameter at the base, attenuated upwards, septate, smooth, pale fuscous below, hyaline above, bearing one or two whorls of phialides towards the apex. The phialides are one-septate, the lower segment being cylindric or ovate,  $18-20 \times 7\mu$ , and the upper segment flask-shaped or lanceolate or conical,  $18-28 \times 6-8\mu$ , terminating in a slender sterigma up to  $20\mu$  long. The conidia are hyaline, broadly cymbiform, ends obtuse,  $9-10 \times 5-6\mu$ , or oval,  $7 \times 5\mu$ .

*Verticillium fuliginosum* Petch, n.sp.—Mycelio primo albo, dein fuliginoso, ab insecto folium in macula nigra tenui percurrente; hyphis crassis,  $5-10\mu$  diam. regularibus, pallide fuscis, septis nigerimis; conidiophoris usque  $500\mu$  alt., infra  $7\mu$  diam. supra attenuatis, septatis, laevibus, infra pallide fuscis, supra hyalinis, phialides in verticillis singulis vel duobus apicem versus ferentibus; phialidibus uniseptatis, articulo infero cylindraceo vel ovato,  $18-20 \times 7\mu$ , articulo superiori ampullaceo vel lanceolato vel conico,  $18-28 \times 6-8\mu$ , in sterigmate tenui, usque  $20\mu$  longo abeunte; conidiis hyalinis, late cymbiformibus, utrinque obtusis,  $9-10 \times 5-6\mu$ , vel ovalibus,  $7 \times 5\mu$ .

On a leafhopper on sugar cane, Surinam and Panama.

95. *SPOROTRICHUM COLUMNARE* Petch, n.sp.

In the Eastern tropics, *Cordyceps dipterigena* B. & Br. is parasitised by two species of *Sporotrichum*, viz. *S. album* Petch and *S. isarioides* Petch. In the Western tropics, another species of *Sporotrichum* has been found

parasitic on entomogenous fungi. This was first observed on a *Hirsutella* on flies, collected by Dr C. B. Williams at Essequibo, British Guiana, November 11th, 1916. Another specimen occurred on a spider cocoon, collected at Maricao, Porto Rico, March 23rd, 1916 (Cornell University, No. 730), and others on *H. entomophila* Pat., on beetles, Moruga, Trinidad, January 14th, 1921 (coll. W. Nowell), and on *H. floccosa* Speare, on froghoppers, Trinidad (E. M. Wakefield). In the spider cocoon, the host fungus was not identifiable.

In addition to a white film over the host fungus and insect, the *Sporotrichum* produces conical or cylindric clavae, scattered or clustered. The peripheral hyphae of these clavae terminate in simple conidiophores, usually geniculate towards the apex. The conidia, however, are not attached at the angles, as in *S. album*, but in a group just above an angle, and also at the apex of the conidiophore. Thus the conidiophore, in general, is geniculate, with minute papillae, the scars of attachment of the conidia, in small numbers just above each bend.



Fig. 6. *Sporotrichum columnare*. Conidiophore and conidium.  $\times 1000$ .

As pointed out in *Trans. Brit. Mycol. Soc.* xvi (1931), 55, *Beauveria Petelotii* Vincens, from Brazil, is evidently *Hirsutella Saussurei* parasitised by a *Sporotrichum*. Vincens, however, figured the *Sporotrichum* as having geniculate conidiophores, with conidia broadly attached at the angles, as in *S. album*. Hence it seems improbable that the West Indian species is the same. I propose the name *Sporotrichum columnare* for the latter.

*Sporotrichum columnare* Petch, n.sp.—Mycelio insectum membrana alba obducente; clavis albis, sparsis vel congregatis, conicis vel cylindraceis, simplicibus vel furcatis, usque 1.8 mm. alt., 0.3 mm. diam., ex columna centrali strato laxo conidiophororum cincta compositis; conidiophoris simplicibus, 1.5–2  $\mu$  diam., flexuosis, supra geniculatis, angulis et apice minute verrucosis, apice clavato vel leniter inflato vel a latere flecto; conidiis hyalinis, angusto-ovalibus vel oblongo-ovalibus, uno fine acutis, 3.5–11  $\times$  1.5  $\mu$ .

On *Hirsutella* spp., West Indies.

96. *SPOROTRICHUM LARVATUM* Peck

In *Sylloge Fungorum*, x (1892), 533, Saccardo entered the description of *Sporotrichum larvatum* Peck, from the *Thirty-second Report of the New York State Museum*, p. 44, as follows:

"Caespitulis confluentibus, densis, mollibus, dein pulverulentis albidis vel flavidis, matricem totam obducentibus; hyphis tenuissimis, simplicibus vel ramosis; conidiis copiosis, minutis, globosis, 2-3 $\mu$  diam. Hab. in larvis sub Alnis, Adirondack Mount. Amer. bor.—'An Botryti Bassianae affinis species?'"

The *Thirty-second Report* was never issued to the public. In the *Thirty-fourth Report* (for 1880, published 1881), the Director of the Museum commented upon the method of dealing with the scientific reports and stated (p. 5) that the scientific papers which accompanied the *Thirty-second Report* had not been published for the use of the Regents or for the Museum, but that the Report only had been printed among the State documents; and again (p. 11) "the *Thirty-second Report*, communicated in January, 1879, is printed simply as a public document, without the illustrations accompanying the scientific papers; no copies having been printed for the Regents or the Museum; and it is essentially inaccessible to the scientific public."

In the *Thirty-third Report* (for 1879, published 1880), Peck entered the name *Sporotrichum larvatum* Pk. in a list of plants new to the herbarium (p. 13).

In *Bulletin of the New York State Museum*, 1, No. 2, p. 18 (May, 1887), Peck published a description of *Sporotrichum larvicolum* in a paper entitled "New Species of New York Fungi." The description is:

"Flocci slender, simple or branched, forming a continuous, dense, soft, white or yellowish stratum coating the whole matrix; spores abundant, minute, globose, 0.00008 to 0.00012 in. broad. Dead larvae lying on the ground under alders. Adirondack mountains. July.... In some specimens the fungus spores were so abundant that the surface of the stratum had a pulverulent appearance."

It will be seen that the descriptions of *Sporotrichum larvatum* and *S. larvicolum* are the same, differing merely in the order of the phrases, and the fungi are on the same host and from the same locality.

In the Bulletin in question, a note on the contents page states, "The titles of the first four articles were enumerated in the *Thirty-seventh Report on the State Museum*, but the articles were not printed. A revision of them is given here." On referring to the *Thirty-seventh Report*, it is found that Peck there stated, "I have also added to this part of the report descriptions of new species contained in the *Thirty-second Report*, but which were never published in such a way as to be generally available to the public, or to those most interested in having them"; and in the Table of Contents there is the title, "Descriptions of

New Species of New York Fungi." Finally, in the *Fortieth Annual Report* (published 1887), the Director of the Museum stated, "Since my report of last year was communicated to the Board of Regents, they have ordered an edition of the *Thirty-second Report* to be reprinted."

Thus Peck wrote his paper, "Descriptions of New Species of New York Fungi" for the *Thirty-second Report*, which was not issued to the public. He included it again in the *Thirty-seventh Report*, but it was omitted. It was finally published in the *Bulletin* in 1887, and the name *Sporotrichum larvatum* was there changed to *Sporotrichum larvicolum*. Confirmation of this is afforded by a comparison of the consecutive names in the paper in the *Bulletin* with those in the *Botanical Index to New York State Museum Reports* 22 to 38, included in the *Forty-first Report*. *Sporotrichum larvicolum* was the first effective publication.

Judging from the description, the fungus is *Beauveria Bassiana*. The dimensions given for the conidia are larger than is usual in that species, but I have examined a specimen of *B. Bassiana* from China, on a silkworm, in which the conidia were  $2\text{--}4.5\mu$  diameter.

I am indebted to Mr E. W. Mason, of the Imperial Mycological Institute, for assistance in ascertaining the data concerning Peck's Reports.

#### 97. *OOSPORA OBDUCENS* Syd.

This species was described by Sydow from the Philippines. It occurred on a Cicada, on which it formed effused, confluent, intense green masses. The conidia were narrow oval or oblong, obtuse,  $9\text{--}13 \times 3.5\text{--}5\mu$ , more rarely subglobose or broadly oval and  $6\text{--}9\mu$  long. The specimen was said to be old and mycelium was lacking.

Except for the occurrence of some subglobose conidia, the details given agree with *Metarrhizium Anisopliae*.

#### 98. *METARRHIZIUM BRUNNEUM* Petch, n.sp.

This fungus, on a Homopterous insect (Cicadellidae), collected at Laguna, Philippine Islands, December, 1931, was kindly sent me by Dr G. O. Ocfemia. It differs from *Metarrhizium Anisopliae* in colour and in the shape of its phialides, and from *M. album* in colour and the absence of a firm convoluted stroma.

*Metarrhizium brunneum* Petch, n.sp.—Insectum pulvare brunneo obducente; stromate basilari exiguo, ex hyphis laxe intertextis composito; phialibus clavatis, usque  $9\mu$  longis, supra usque  $2\text{--}3\mu$  diametro incrassatis; conidiis cylindraceis vel anguste ovalibus, utrinque rotundatis,  $4\text{--}6 \times 1.5\text{--}2\mu$ , leviter flavis, coacervatis brunneis, catenulatis. Ad Homoptera (Cicadellidae), Philippine Islands.

The chains of conidia are laterally adherent in broad masses, which split into columns of spores, as in *M. Anisopliae*.

99. *CLADOSPORIUM*

In *Symbolae Mycologicae*, p. 356 (1869), Fuckel enumerated *Cladosporium herbarum* var. *Aphidis* Fuckel, without description. It occurred on dead aphids on *Cornus sanguinea* in Austria.

In 1877, Thuemen described a *Cladosporium* on aphids as *Cladosporium Aphidis*. This was included in Saccardo, *Sylloge Fungorum*, with a note that it might be the same as *Cladosporium herbarum* var. *Aphidis*, but it was certainly very different from *C. herbarum*.

In *Fungi Veneti*, v, 191, and *Mycotheca Veneta*, No. 587, Saccardo distributed specimens which he referred to *Cladosporium penicilliooides* Preuss. These had been collected at Selva, Treviso, "in chrysalidibus ad folia adhuc pendula *Pruni domesticae*, Sept. 1875." In the copy of *Mycotheca Veneta*, No. 587, in Herb. British Museum, the fungus is on aphids, and it does not differ from that usually attributed to *Cladosporium Aphidis*. *C. penicilliooides* was described by Preuss from specimens growing on *Tubicularia granulata* and *T. vulgaris*. It has been included among entomogenous fungi on the basis of Saccardo's record, and it should now be discarded.

In *Revue Mycologique*, 1890, p. 132, Briard and Hariot described *Cladosporium Aphidis* var. *Muscae*, found on a fly in France.

Giard in 1889 (*Bull. Sci. France et Belge*, xx, 217), instituted a new genus, *Polyrrhizium*, with the species, *P. Leptophyei*, for a fungus on an Orthopteron which he had previously referred tentatively to *Metarrhizium*. Giard was doubtful whether the fungus was not saprophytic, but decided that it was parasitic because the position of the dead insects was that assumed by insects attacked by parasitic fungi. A probable explanation of that is indicated below. There is little doubt, from Giard's figures and description, that the fungus was a *Cladosporium*. Giard himself stated that perhaps *Polyrrhizium* should be referred to *Cladosporium* or *Alternaria*, and that that would be another reason for considering it a saprophyte.

In 1891, Giard published a paper, entitled "Sur les Cladosporiéees entomophytes, nouveau groupe de Champignons parasites des Insectes" (*Compt. Rend.* June 29th, 1891). This was a biological group, including, *inter alia*, Giard's genera, *Polyrrhizium* and *Penomyces*. He claimed that these fungi killed insects by blocking the tracheae.

In 1893, Rostrup (*Vidensk. Medd. naturh. Foren i Kjøbenhavn*, p. 95) remarked that Thuemen had described a *Cladosporium Aphidis*, which attacked aphids. Rostrup added that the occurrence was not uncommon, but the fungus was scarcely an independent species, confined to aphids, but a form of the ubiquitous *Cladosporium herbarum*, which had derived its nourishment from honeydew, whereby it grew very vigorously and spread over diseased or dead aphids.

Also in 1893, Giard (*Bull. Sci. France et Belg.*, xxiv, 106) expressed the opinion that *Cladosporium Aphidis* Thuem. was only a variety of *C. herbarum*, viz. *C. herbarum* var. *Aphidis*.

Guéguen (*Champignons parasites*, 1904) recorded *Cladosporium herbarum* on a *Chermes* on *Mesembryanthemum edule*. According to Picard (*Ann. l'École Nat. d'Agric. Montpellier*, n.s., xiii (1914), 208), the name of the insect should be *Pulvinaria mesembryanthemi*. Guéguen suggested that the "Cladosporiées entomophytes," if not purely saprophytic, penetrated the insect only after it had been attacked by another parasite, *Entomophthoraceae* or perhaps bacteria.

In 1918, C. Massalongo described *Cladosporium herbarum* var. *aphidicola*, found on aphids on *Sonchus* in Italy. In *Sylloge Fungorum*, xxv (1931), 798, it was suggested that this is the same as *Cladosporium herbarum* var. *Aphidis* Fuckel, which was *nomen nudum*.

In 1923 (*Congrès Path. Veg. Strasbourg*, p. 48), Raybaud recorded, under the name *Cladosporium Lauri*, a fungus which had been found on the scale insects, *Aonidia lauri* and *Lecanium hesperidum*, on *Laurus nobilis*.

Giard's genus, *Penomyces*, was not entered in the *Sylloge Fungorum* until 1913 (vol. xxii). Giard did not give formal generic or specific descriptions, and it is scarcely possible to decide from his discursive accounts what he considered the essential characters of his genera. Guéguen (*Champignons parasites*) made an attempt to remedy Giard's omissions by summarising the facts given in his papers, but the data are really insufficient for precision, and one is still left wondering why Giard considered it necessary to create new genera.

In 1914 (*Ann. Myc.* xii, 295), Saccardo described, as *Penomyces cladosporiaceus*, a fungus found on mites on *Datura* in Moravia. Saccardo stated that *Penomyces* seemed to be distinguished from *Cladosporium* by having its conidia for the most part subglobose and continuous. Giard, however, did not describe the conidia of *Penomyces* as subglobose, and the dimensions which he gave for the species are not in accordance with that view. Saccardo's fungus would appear to differ from the common *Cladosporium* on insects, but it might still be included in that genus.

From the few details available, *Cladosporium parasiticum* Sorokin, found on a beetle, *Melolontha fullo*, in Russia, does not appear to be a *Cladosporium*.

Summarising the foregoing details, it is found that the *Cladosporiums* which occur on insects have been referred to the following species:

On aphids:

*Cladosporium herbarum* var. *Aphidis* Fuckel; also by Giard.

*Cladosporium Aphidis* Thuem.

*Cladosporium herbarum* Link, by Rostrup.

*Cladosporium aphidicola* Massalongo.

*Cladosporium penicilliodes* Preuss; in error.

On scale insects:

*Cladosporium herbarum* Link; by Guéguen.

*Cladosporium Lauri* Raybaud.

On Orthoptera:

*Polyrrhizium Leptophyei* Giard.

On Coleoptera:

*Penomyces telaria* Giard.

*Penomyces Cantharidum* Giard.

*Cladosporium parasiticum* Sorokin.

On Hemiptera:

*Penomyces telaria* Giard.

On Diptera:

*Cladosporium Aphidis* var. *Muscae* Br. & Har.

On Acari:

*Penomyces cladosporiaceus* Sacc.

With the exception of *Cladosporium parasiticum* and *Penomyces cladosporiaceus*, these appear to be all the same species.

Rostrup stated that *Cladosporium herbarum* developed luxuriantly on honeydew, and spread thence to dead aphids. That the same *Cladosporium* grows both on honeydew and on aphids is true. I have observed this in aphids on beech leaves, on which the fungus grew on insect-free patches of honeydew and also on the aphids. But the fungus hyphae did not extend from the honeydew to the insects. The two growths were separate, though on the same leaf. Moreover, as a rule, the *Cladosporium* is not found growing on the leaf.

The *Cladosporium* which occurs on dead flies is undoubtedly the same morphologically as that on aphids, and on the former it usually follows an attack of *Empusa* or *Entomophthora*. It frequently happens that flies are killed by one of the Entomophthoraceae, but, probably because of a change in weather conditions, the insect dries up before the conidiophores of the fungus have emerged. Such individuals often bear *Cladosporium*.

That *Cladosporium* followed an attack of *Entomophthora* was suggested by Guéguen, who pointed out that that hypothesis would explain the facts noted by Giard in *Polyrrhizium Leptophyei* and *Penomyces Cantharidum*, viz. that the insects which Giard supposed were killed by these fungi died in the attitudes assumed by insects killed by Entomophthoraceae. It is almost impossible in such instances to determine the presence of the latter in the desiccated insect. In one instance, I found a dead fly attached to a leaf by its proboscis, after the manner of *Empusa Muscae*, but the only fungus recognisable was a minute tuft or nodule of *Cladosporium* at the tip of the proboscis.

As previously noted (*Trans. Brit. Mycol. Soc.* xvi (1932), 229),

*Lecanium viride*, in Ceylon, South India and Java, when attacked by *Empusa Fresenii*, is soon overrun by *Cladosporium* and other Dematiae, and it is difficult to find the *Empusa* on the insect. Similarly, in the Philippines, aphids attacked by the same *Empusa* have been quickly covered with *Cladosporium*. The growth of Dematiae in these cases is much more rapid than that on flies killed by Entomophthoraceae in Britain.

There is no doubt that *Cladosporium* will grow freely on insects killed by Entomophthoraceae, but it is open to question whether that will explain all occurrences of *Cladosporium* on insects.

Fuckel's name, *Cladosporium herbarum* var. *Aphidis* has been rejected as *nomen nudum*, as it was published without a description. Fuckel probably considered that the fungus did not differ from *C. herbarum*, except as regards its host.

#### 100. A STERILE STROMA

A fungus which forms brown circular discs covering individual specimens of *Aspidiotus* was collected at Nuwara Eliya, Ceylon, on several occasions during 1926-8, principally on *Psychotria*, but in no instance was the fructification found.

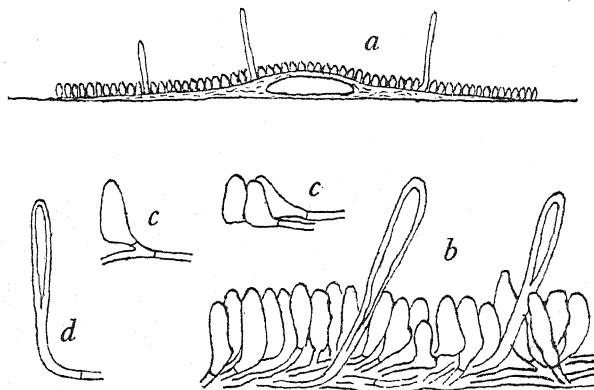


Fig. 7. A sterile stroma. *a*, cross-section (diagrammatic),  $\times 40$ ; *b*, part of radial cross-section,  $\times 250$ ; *c*, superficial cells,  $\times 250$ ; *d*, a seta,  $\times 250$ .

The discs are circular, up to 3 mm. diameter, seal-brown with a paler fimbriate margin, becoming dark brown, minutely tomentose, flat, pulvinate in the centre, about  $40\mu$  thick, increasing to  $150\mu$  in the centre over the scale insect. They consist of a basal stratum of radial hyphae, which are brown, regular,  $3\mu$  diameter, to a thickness of about  $10\mu$ , but forming a thicker weft over and round the scale.

From this stratum arise shortly stalked, erect, brown cells, 20–30  $\mu$  high, 10–15  $\mu$  diameter, usually conoid with an obtuse apex, sometimes clavate and rounded above, closely packed side by side in a palisade layer, which, however, may be lacking over the scale. In addition, there also arise from the basal layer, dark brown, thick-walled setae, up to 200  $\mu$  high, 10  $\mu$  diameter, elongated clavate or cylindric, usually attenuated towards the base, darker than the palisade cells and sometimes almost sessile.

Some specimens bear small purple-red nodules. These are pauperate sporodochia of *Pseudomicroceria Henningsii*, growing on the scale insect, which have been partly overgrown by the brown fungus. No conidia, sporophores, or basidia of the brown fungus have been observed.

The fungus differs from a *Septobasidium* in that the stromata do not extend and coalesce. The setae suggest *Hymenochaete*, though they are not typical *Hymenochaete* setae, but no basidia have been found.

#### CORRECTIONS

The conidia of *Oospora subfasciculata* Petch (*Trans. Brit. Mycol. Soc.* xvi (1931), 63) are 2–3  $\times$  1–1.5  $\mu$ , not 2–3  $\times$  1.1–5  $\mu$  as originally printed.

The height of the perithecia of *Ophiocordyceps acicularis* is 0.48 mm., not 0.28 mm. as given in *op. cit.* xviii (1933), 60.

*PORIA PEARSONII PILÁT SP.N.*

By DR ALBERT PILÁT

(National Museum, Prague)

(With Plate III)

IN August 1933 and 1934, when collecting in Carpathian Ruthenia, I found in surprising abundance a *Poria* covering the prostrate trunks of *Abies alba* in a wood near the Kuzy brook at Velký Bočkov, a small town on the border of Czechoslovakia and Roumania, at a height of about 800 metres above the sea.

This *Poria* proved to be identical with that which Mr A. A. Pearson had doubtfully determined as *P. medulla-panis* Fries (non Persoon) and sent to Bourdot under that name (Bourdot in *Bull. Soc. mycol. Fr. XLVIII* (1932), 231).

This fungus in the dried state is coriaceous and more or less stratose, but when fresh is softer and saturated with water. It is a species that has been overlooked, though distributed throughout Europe and Northern Asia, especially in mountainous regions. Specimens have been gathered by Murashkinsky in Siberia and by Litschauer from two localities in Austria as mentioned in a letter to me.

## DESCRIPTION OF THE CARPATHIAN SPECIMENS

*Poria Pearsonii* Pilát sp.n.

Receptacle widely effused, confluent and often completely covering the prostrate trunks of trees, closely adherent but occasionally separating in places, when fresh white, watery-spongy, subfleshy then hard; in the dried state coriaceous, with the margin often slightly raised and subundulate. Subiculum of fine structure, membranous, white, irregular and penetrating into the fissures of the bark.

Tubes 2-5 mm. long, in most specimens more or less stratose in two to four layers; when fresh white, in dried specimens creamy or yellowish, brownish where rubbed.

Pores concolorous, angular-round, 0.12-0.40 mm. diameter or 0.50-1 mm. long.

Margin similar, often slightly raised in adult specimens.

Hyphae densely interwoven 2.5-3  $\mu$  thick, rarely 5-6  $\mu$  in subiculum more loosely compacted, horizontal.

Basidia  $10-12 \times 5-6 \mu$ . Cystidia fairly numerous but not conspicuous, thick-walled  $24 \times 7 \mu$ , projecting 5 to  $10 \mu$ , clavate-subfusoid, smooth or more often with apex incrusted with crystalline granules.

Spores not found in Siberian specimens, but in those gathered by A. A. Pearson in Somerset, England, on log of *Pinus sylvestris* October, 1929, and sent to Bourdot, the spores were widely elliptical or ovate,  $3.5-4.5 \times 2.5-2.75 \mu$ : in Carpathian specimens, ovate,  $3.7-4.2 \times 26-27 \mu$ .

*Habitat.* On prostrate trunks of *Abies alba* in Czechoslovakia—Carpathian Ruthenia, near the Kuzy brook above Velký-Bočkov July and August, 1933 and 1934, in great abundance.

On the bark of trunks of *Abies sibirica* in Siberia, district Kuznetzk, September 29th, 1930, collected by Krawtzew, and sent by Professor Murashkinsky.

We dedicate our species to Mr A. A. Pearson.

#### LATIN DIAGNOSIS

##### *Poria Pearsonii* Pilát sp.n.

? *Poria medulla panis* Fries (non Persoon) comp. Bourdot, *Bull. Soc. mycol. Fr.* XLVIII (1932), 231.

Exsiccata: A. Pilát: *Fungi carpatici lignicoli*, no. 129.

*Carposomata* late effusa, confluentia et totos truncostratos saepe obtegmentia, sat firme accreta, solum in fragmentis *subseparabilia*, in *statu vivo alba*, *aqueo-spongiosa*, *subcarnosa*, dein indurantia, exsiccata coriacea et marginibus saepe paulisper relevata et subundulata. Subiculum (trama) tenuissimum, membranaceum, album, irregulare, in rimas corticis penetrans.

*Tubuli* 2-5 mm. longi, in exemplaribus majoribus *plerumque stratosi* (bi-usque tetrastrosi), *albi*, exsiccati *cremei*, sublutescentes, in locis vulneratis saepe *subbrunnescentes*.

*Pori* concolores, angulato-rotundati, 0.12-0.4 mm. diam. vel 0.5 ad 1 mm. longi.

*Margo* similis, saepe in carposomatibus adultis paulisper relevatus.

*Hyphae* crasse tunicatae usque solidae,  $2.5-3 \mu$  crassae, rarius usque  $5-6 \mu$ , in subiculo sat laxe intricatae, horizontales, hyphae dissepimentorum subverticatae, dense intricatae.

*Basidia*  $10-12 \times 5-6 \mu$ . Cystidia *sat crebra*, sed haud conspecta, crassius tunicata,  $24 \times 7 \mu$  ca. magna,  $5-10 \mu$  prominentia, *clavato-subfusoides*, laevia vel saepius *capitulo* *crystallino* calcii oxalatici *coronata*.

*Sporae* in speciminibus Sibiricis haud observata. In speciminibus

carpaticis anno 1934 lectis sporas ovoideas,  $3\cdot7-4\cdot2 \times 2\cdot6-2\cdot7 \mu$  magnas observavi. In speciminibus britannicis a cel. A. A. Pearson prope Somerset Britanniae ad ligna *Pini* Oct. 1929 lectis cel. Bourdot sporas late ellipsoideas vel ovoideas  $3\cdot5-4$  ( $4\cdot5$ )  $\times 2\cdot5-2\cdot75 \mu$  observavit.

Three large trunks, about 1 metre thick, of *Abies alba* were found by me entirely covered with the fungus. When fully developed, it is stratose, but the layers are never regular. It differs from *Coriolus obducens* (Pers.) in its appearance, the pores never acquiring when dry the attractive yellow tint found in *C. obducens*, which in its resupinate form is the same as *C. connatus*.

Some British mycologists, according to Bourdot (*loc. cit.*) have considered the fungus to be *Poria medulla-panis* sensu Fries non Persoon. The description, however, in Rea's *British Basidiomycetæ* does not agree with our fungus and probably represents the true *P. medulla-panis* of Persoon. We also know that the specimen of *P. medulla-panis* in the herbarium of the Royal Botanic Gardens, Kew, appears to be the species of Persoon.

The *medulla-panis* of Fries in his *Systema mycologicum*, I, 380, is thus described "effusus subundulatus, durus, glaber, siccus, albus, poris mediis. Ad ligna prostrata rario.".

This is a very brief diagnosis and corresponds more or less with both fungi. But Fries uses the word "durus" and this agrees more with the true *Poria medulla-panis* of Persoon than with our fungus which when fresh is fairly soft, spongy-watery and somewhat fleshy.

In *Mycologia Europaea*, II (1825), 100, the description agrees with the true *Poria medulla-panis*, and Persoon cites Fries in the synonymy.

A species very near to our fungus is *Poria subacida* Peck (Saccardo, *Syll. Fung.* VI (1888), 325. Syn. *Polyporus (Physisporus) subacidus* Peck in 38th *Rept. N.Y. State Mus.* pp. 92-3 (1885)) which is fairly common all over North America on coniferous wood. I have compared *Poria Pearsonii* with the accurate description and with the photographs of the original specimen of *P. subacida* which were published by Overholts in the *New York State Mus. Bull.* No. 205-6 (1919), pp. 111-15, t. 19, 20, 21, f. 6, together with the description and figures of specimens found by Shope in Colorado (Shope in *Ann. Missouri Bot. Garden*, XVIII (1931), 399, t. 39, f. 3), and also with the specimens in my private herbarium of this species on *Pinus virginiana*, mouth of Scott Run, Arl. W. Va. Coll. det. by J. R. Weir, November, 1922, and also on a log in a swamp at Vermihen, Mich., July, 1914, leg. A. Povah det. Overholts. *Poria subacida* Peck has a smoother surface of a darker yellowish brown. The hyphae in the dried specimens are always more or less yellow or yellow-brown, while in our species they are hyaline under the microscope. The American specimens of *P. subacida* which I have produced spores abundantly, while those of *P.*

*Pearsonii* are apt to be sterile; the stratification of adult specimens of *P. subacida* is also not so conspicuous and the sterile margin is more distinct; further in *P. Pearsonii* there is no marked marginal differentiation. In the texture of *P. subacida* I found quantities of crystals of calcium oxalate which Overholts and Shope mention, but the cystidia are indistinct and without incrustation. On the other hand *P. Pearsonii* has no crystals in the texture, but has cystidia with globose incrustations distinctly visible.

*P. corticola* Fries is nearly related, but certainly not the same (Pilát in *Bull. Soc. mycol. Fr.* XLVIII (1932), 38). This species grows on the bark of frondose trees, especially *Populus tremula*, and has characteristic cystidia.

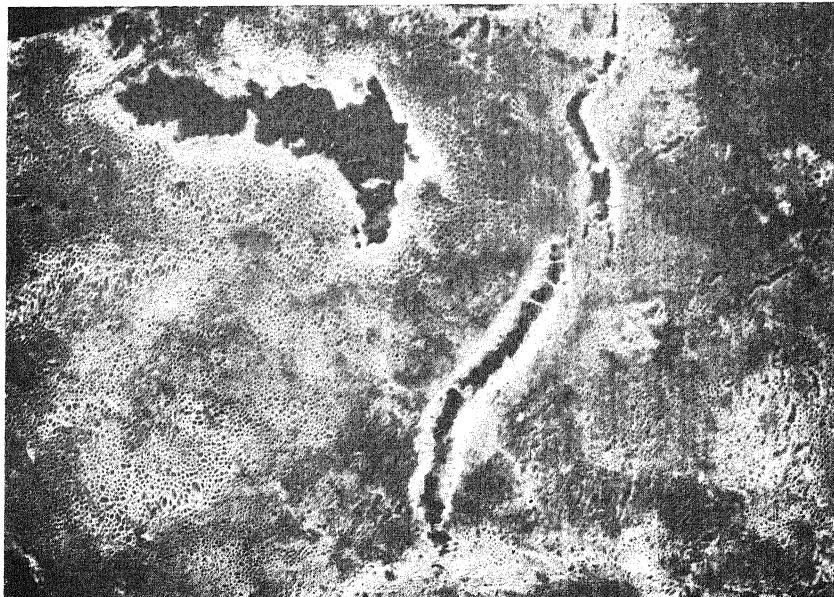
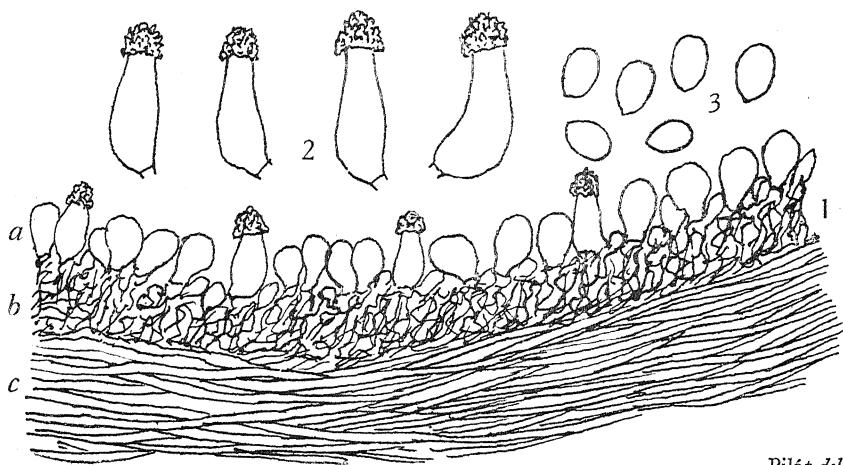


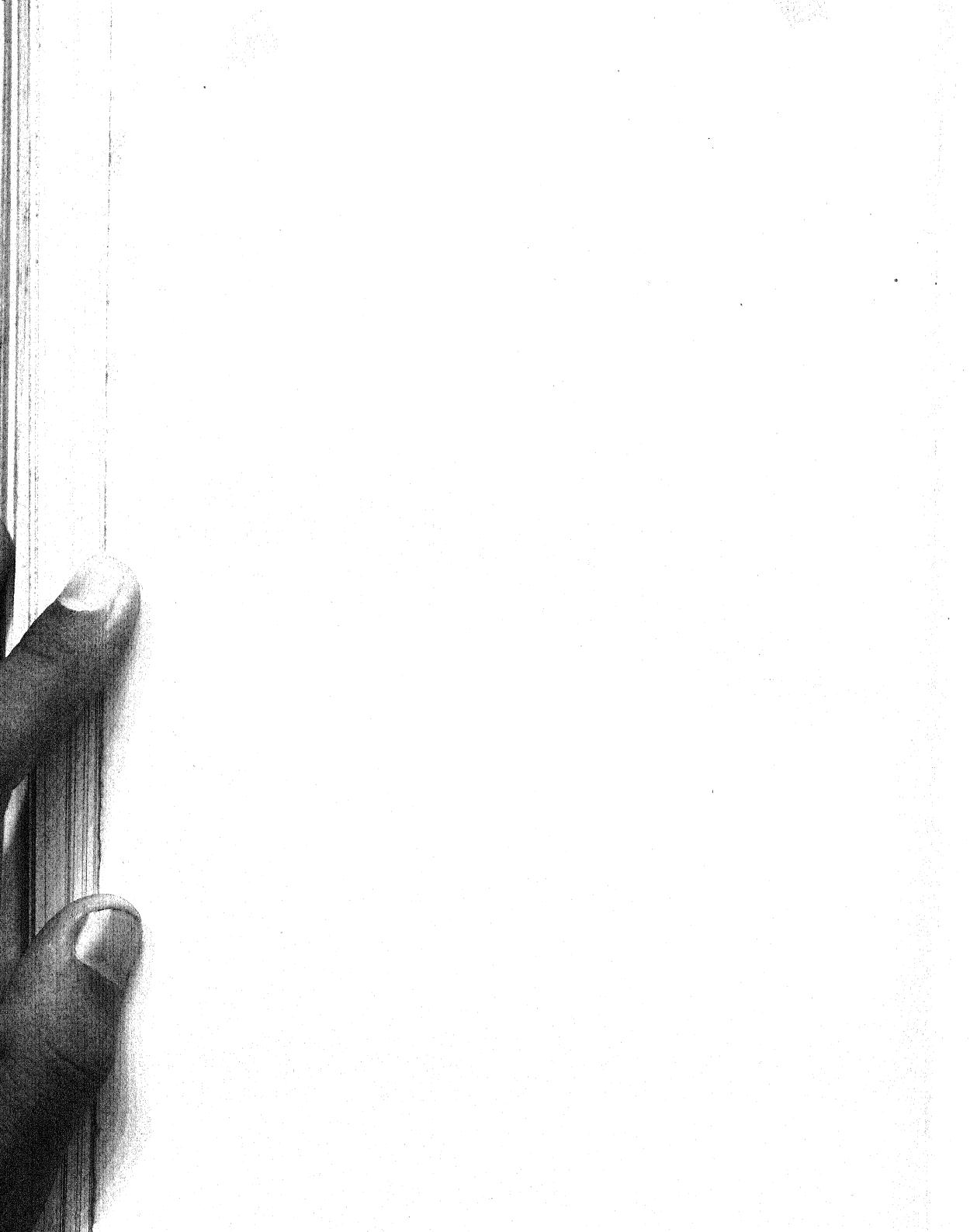
Photo A. Pilát

Fig. 1. *Poria Pearsonii* Pilát. Ad corticem truncorum prostratorum *Abietis albae* Mill. Cechoslovakia-Carpatorossia, ad rivum Kuzy supra Velký Bočkov, 1933.-VII.



Pilát del.

Fig. 2. *Poria Pearsonii*. 1, Hymenium in sectione; a, Basidia et cystidia; b, Subhymenium; c, Mediostratum. 2, Quatuor cystidia; 3, Sporae.



# ON *LAMBERTELLA CORNI-MARIS* VON HÖHNER, A BROWN-SPORED PARASITIC DISCOMYCETE

By T. H. HARRISON, D.Sc. AND  
A. F. EL-HELALY, B.Sc., PH.D.

(With Plate IV and 4 Text-figures)

## INTRODUCTION

IN August, 1931, the senior author made a tour of some of the deciduous fruit areas of Western Europe with the object of studying the incidence of "Brown Rot" in fruits and of collecting material for critical studies of the organisms concerned. Search was made at all suitable points for apothecia arising from fruits mummified by the various organisms.

Some apothecia found on mummified apples in Switzerland, and others on mummified pears at two places in South Germany, 160 kilometres apart by road, appeared in the field to belong to *Sclerotinia fructigena* Ader. & Ruhl., a species for which apothecia have only once<sup>(1)</sup> been carefully described. Subsequent examination showed that the ascospores were brown, and further experience indicated that the fungus was *Lambertella Corni-maris* von Höhnel. This species was first found by von Höhnel, in 1917, on mummified fruits of the cornelian cherry (*Cornus Mas* L.) in Austria. A comparison of the material collected in 1931 with von Höhnel's type material showed that the samples were co-specific.

The fungus is of interest to plant pathologists, inasmuch as it causes a firm brown rot and mummification of several common fruits, and it has an exceptional tolerance of acidity. In pure culture on artificial media it readily forms apothecia in the laboratory, a point of interest to mycologists and teachers.

The senior author is responsible for the account of the occurrence, morphology and taxonomy of the organism; the junior author for the bulk of the cultural, physiological and pathological studies.

## OCCURRENCE AND DESCRIPTION OF APOTHECIA

The first batch of apothecia was found on mummified apples beneath a neglected apple tree on a hillside at Viège near Brügg, in the Upper Rhine Valley, Switzerland. The fruits on the tree were heavily infected with *Sclerotinia fructigena*. Mummified fruits lay in

abundance beneath the tree, some freshly formed, others at least a season old. Search in a moist, neglected spot on the lower side of the tree yielded apothecia, some on blackened mummified apples, some on unidentified fragments. The moisture and temperature of the locality were very similar to those which experience in Australia had shown to be ideal for the production of apothecia by *Sclerotinia fructicola*. It was considered at the time that these Swiss apothecia belonged to *Sclerotinia fructigena*, and it was felt that the opportunity of checking the description of this fungus by Aderhold and Ruhland should not be lost. As this was impossible at the time, material was sent to the Imperial Mycological Institute, Kew, where it was examined by Mr S. P. Wiltshire, whose notes are incorporated in this paper. He found that the ascospores were brown, and placed the fungus in the genus *Lambertella*.

Many of the apothecia were immature when collected, but Mr Wiltshire brought these to maturity, and induced others to develop, by keeping the mummified fruits in moist sand at 18–20° C. One of these fruits is shown on Pl. IV, fig. 1.

The fruit body was first visible as a minute sphere with the position of the disc discernible; it then elongated to a drum-stick-like object which expanded at the top to give the mature apothecium. The stipitate apothecia were at first crateriform, then saucer-shaped, and later flattened. Their colour varied with the location and age of the disc; some were pale pink to flesh coloured, others buffy citrine (Ridgway, Plate XVI), and others were dark brown. The disc ranged in diameter from 1 to 5 mm. The margin of the disc was uniform, obtuse and glabrous, except in young stages, when a few simple hyaline hairs were present. The apothecia were positively phototropic. The stipe varied considerably in length. Some apothecia were nearly sessile, others had a stipe 3 cm. long. The stipe arose from the blackened mummified fruit, and was black and very thin at the base, the extent to which these characters were present varying from specimen to specimen. The stipe became thicker and lighter in colour until it reached the bottom of the disc; this was lighter than the upper surface. The stipe was hairy, especially towards the base; rhizoids were absent.

For long distances in Switzerland and in South Germany the roads are lined with fruit trees, mainly apples and pears. Most of the trees are old and neglected. "Brown Rot", mostly caused by *Sclerotinia fructigena*, is prevalent in places and many mummified apples and pears can be found in warm, moist depressions beneath trees growing on sunny slopes, where dense herbage is usual. Apothecia were found on mummified pears from the previous season's crop in two situations of this sort, one by the side of the main road from Basle to Freiburg, the other on a grassy slope near the main road

from Freiburg to Baden-Baden. One pear, bearing twenty-one apothecia in various stages of development, was photographed *in situ* (Pl. IV, fig. 2). Another pear showing more clearly the details of stipe and disc is shown on Pl. IV, fig. 3.

The apothecia from the mummified pears were generally larger than those found on the apples in Switzerland. They were disciform to flat, flesh-pink to pale brown, and ranged in diameter from 1.5 to 7.5 mm. The stipe ranged in length from 0.5 to 20 mm., tapering gradually from the disc to the point of origin in the fruit; its colour graded from that of the disc to the jet-black of the substratum.

The details which follow apply equally to the apothecia from apples and pears, as it has been found that both belong to the same species.

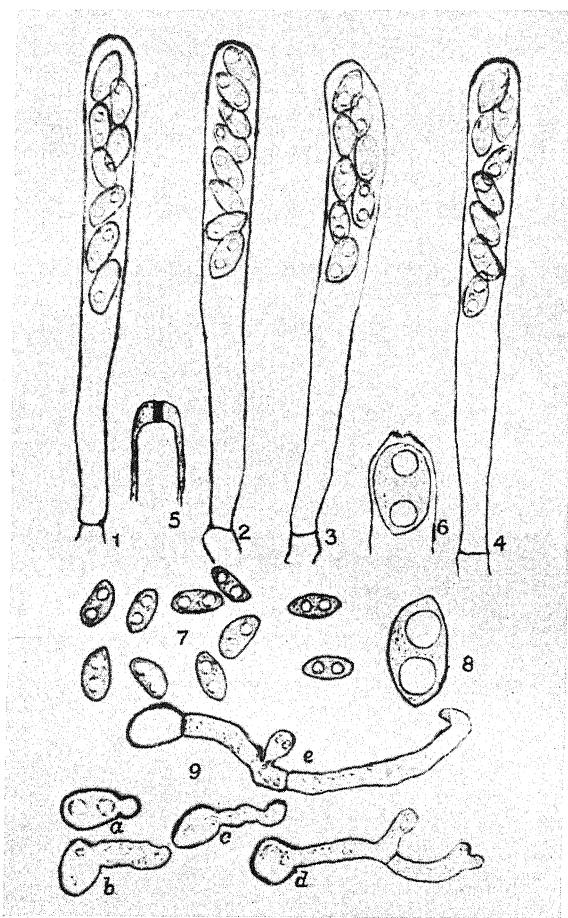
*Asci.* The asci are almost clavate and shortly stalked (Text-fig. 1, 1-4). The apex is somewhat flattened, with a centrally placed cylindrical pore which stains slightly with iodine. In young asci the apex is thickened, but this is much reduced at maturity (Text-fig. 1, 5-6). The asci measure  $80-110 \times 7-8 \mu$  (widest diameter), tapering to  $3-4 \mu$  at the base. Average measurements are  $100 \times 7.5 \mu$ .

*Paraphyses.* The paraphyses are colourless, sparsely septate, only slightly if at all swollen apically, usually unbranched, and projecting a little above the asci. They measure  $100-120 \times 1.4-3 \mu$ .

*Spores.* The spores are irregularly ovoid, mostly somewhat flattened on one side, light brown in the centre, dark brown at the ends. Each spore contains two conspicuous rounded vacuoles, one towards either end of the spore (Text-fig. 1, 7-8). Occasionally the spores are colourless, but these are rare in mature asci. In young asci, the pigment appears to lie in the protoplasm of the ascus, the spores at that time being small, hyaline and very thin-walled. As the spores mature, the colour of the spore wall intensifies while the ascus becomes entirely hyaline. The spores measure  $7.5-11.5 \times 4-6.5 \mu$ ; the average of two hundred measurements was  $9.8 \times 5 \mu$ . The spores are commonly monostichous, but just before discharge they become distichous. Care is required in mounting the preparation if the distichous arrangement is to be seen, as the slightest extra pressure causes discharge of the spores. It does not appear that the manner of arrangement of the spores in the ascus has any taxonomic significance in this type of fungus.

*Germination of the ascospores.* The ascospores germinate readily in distilled water and in many artificial media provided that the temperature is not too high for the fungus. The optimum temperature for growth and for spore germination is about  $20^{\circ}\text{C}$ . At this temperature, germination proceeds rapidly. Usually, a small swelling appears towards one end of the spore, the swelling enlarges, the spore assumes an angular outline and usually a single germ tube is produced. This

may become sinuous, or it may extend straight out for a considerable distance, usually branching laterally, and soon becoming septate (Text-fig. 1, 9 a-e).



Text-fig. 1. *Lambertella Corni-maris* von Höhnel. 1-4, Asci, showing arrangement of the spores. Camera lucida drawing from fresh material in distilled water,  $\times 1000$ . 5, Thickened apex of young ascus, with central core which stains blue with iodine. The contents of the ascus at this stage are brown. 6, Apex of mature ascus, with a spore approaching the central pore; the wall thickening has disappeared. (5-6 drawn by Mr S. P. Wiltshire.) 7, Ascospores,  $\times 1000$ . 8, A typical ascospore; one side somewhat flattened, and ends slightly pointed; vacuoles prominent. Camera lucida,  $\times 2000$ . 9 a-e, Ascospores germinating in distilled water. Camera lucida,  $\times 1000$ .

## CULTURAL BEHAVIOUR OF THE FUNGUS

The organism grows readily on a large variety of media. On synthetic agar media such as Coons's, Brown's or Richards's and on the usual decoctions such as potato agar with or without dextrose, malt agar, etc., the fungus develops rapidly growing circular colonies which are practically devoid of aerial mycelium. On sterilised plugs of tissue such as potato, beetroot, carrot, apple or parsnip a powdery type of white aerial mycelium is shown.

While growth is free on a large variety of media, comparative tests showed that, judged by linear growth rate or by increase of dry weight of mycelium, the most favourable medium is one containing glucose and peptone as sources of carbon and nitrogen respectively. In the young stage the colony appears light yellow and the centre as a rule remains so throughout. Some little distance from the centre a darker zone arises after a time and this extends outwards with the progressive growth of the culture, the growing edge being still light coloured. The dark region becomes darker as the culture ages and in old cultures is almost black, especially on potato media.

After a time—about ten days in cultures incubated at 20° C. and longer at lower temperatures—thick dark brown pseudo-sclerotial crusts develop here and there over the surface of the culture. These are most prominent on potato and malt agars, the whole surface becoming more or less covered with a continuous thick skin.

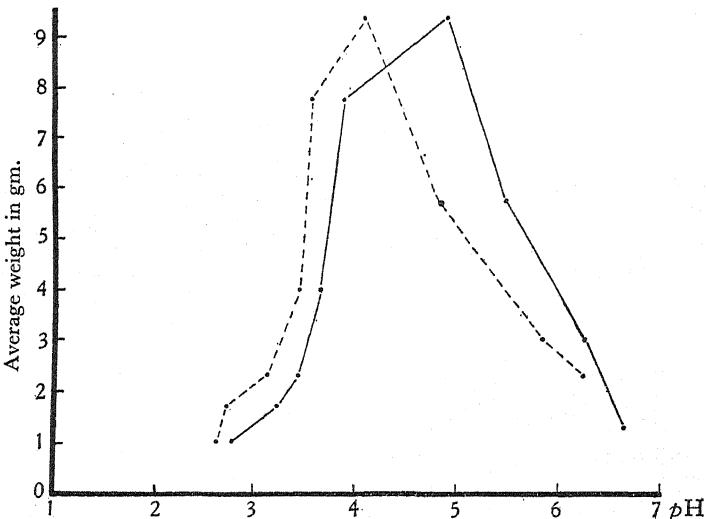
This crust gives rise later to the small spherical bodies which elongate to form immature apothecia: they are very similar to the female receptive bodies mentioned by Drayton(2), being possessed of numerous trichogyne-like hairs. Many become mature apothecia (Plate IV, fig. 4), the disc turning brown as the asci ripen. Sclerotia similar to those found on inoculated fruits have not been observed on artificial media. The sclerotial crust is not due to an accumulation of many small sclerotia, but is formed by the thickening of a dark brown surface incrustation. Ascospore clouds are readily obtained from apothecia growing in culture, and from such clouds it is possible to collect the spores on an inverted agar plate and to isolate the germinating spores. This provides a rapid and efficient method of obtaining single spore cultures.

The markedly acid-loving nature of this fungus is illustrated in Text-fig. 2, which gives the relation of initial  $\rho$ H of the cultural medium (Brown's solution) to the dry weight of mycelium produced. Whether the  $\rho$ H is determined electrically or colorimetrically, it is clear that the optimum for growth lies in the neighbourhood of  $\rho$ H 4-5.

Further experiments with agar media showed that the range of acidity over which growth takes place is  $\rho$ H 1.6-8.3, that the optimum for linear growth is at  $\rho$ H 4.4, and that vigorous growth occurs over

the range  $pH$  3-7. In this respect *Lambertella* recalls the behaviour of the brown-rot fungi generally, as recently worked out by Hall (4).

The general tendency in the growth of this fungus is towards the development of greater acidity in the medium. When the initial reaction of the medium is on the alkaline side of the optimal point, the tendency during growth of the fungus is for the reaction to drift towards greater acidity. Thus on a starch-peptone medium adjusted to different acidities within the range  $pH$  1.8-8.3, there was a drift of 0.5-1 unit towards the acid side in all the media of initial  $pH$  5.9-8.3. Elsewhere the acidity remained unchanged.



Text-fig. 2. Illustrating effect of acidity upon mycelial growth of *Lambertella*.  
 — Colorimetric method. - - - Electric method.

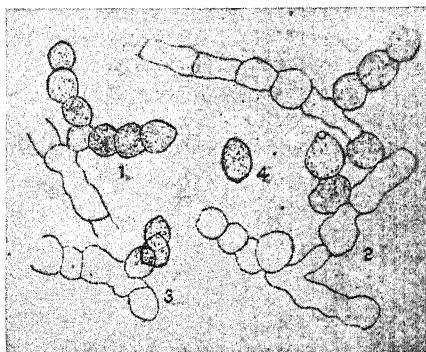
The general appearance of the culture varies according to the acidity of the medium. On starch-peptone agar medium with an acidity of 5.4 or less, the cultures present a clear glassy surface without trace of aerial mycelium and the medium is stained brown. With increasing acidity tufts of white aerial mycelium begin to appear, and over the range  $pH$  4.4 to 2.4 the cultures present a white powdery appearance due to the development of abundant short aerial mycelium. The brown colour characteristic of less acid media has disappeared. At still higher acidities ( $pH$  1.6-2.4) aerial mycelium again disappears on account of reduced growth.

The optimum temperature for growth was found to be near  $20^{\circ}C$ . The maximum temperature is unusually low, viz.  $25^{\circ}C$ . Only on Richards's solution agar was there any appreciable growth at the latter temperature.

## SPORULATION IN CULTURE

Oidium-like chains have been observed on certain media when the cultures have become rather old, *e.g.* in twenty days' old cultures on Richards's agar and one-month old cultures on Brown's A medium. On both media the cultures had become stale and showed a marginal fringe of short white aerial hyphae. In this marginal zone the oidium-like bodies were found in abundance. In no case, even after repeated examination, were they seen in young actively growing cultures.

These bodies appeared as typical oidia (Text-fig. 3) but were not seen to fall apart as separate spores, so that their significance is uncertain. Sometimes they appeared to be germinating *in situ*. From



Text-fig. 3. Monilioid chains (1-3) formed on hyphae of *Lambertella* in culture; 4, isolated conidioid body. Camera lucida drawing,  $\times 1000$ .

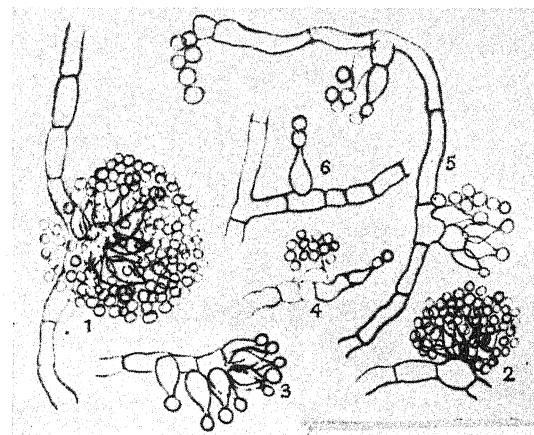
their mode of occurrence they may be looked upon as structures due to staling effects. They are very reminiscent of the similar structures seen in *Moniliopsis Aderholdi*.

*Microconidia* are at times produced abundantly in clumps as illustrated in Text-fig. 4. The heaviest production so far noticed has been on 2 per cent. plain agar, kept at 20° C. for seven days. They are produced in long fragile chains on flask-like structures. Usually the clumps are formed laterally on relatively thin, somewhat coiled, closely septate hyphae, but they may be terminal in origin. Most of the microconidia when abstracted are hyaline, thin-walled, spherical bodies approximately  $3\mu$  in diameter. Germination of these bodies has not been observed.

*Apothecia* are freely produced on a variety of media under suitable conditions. The primordium of the fruit body appears as a minute dark brown outgrowth from the superficial crust of mycelium. This

elongates, reaching its full length in about five days, after which the apothecial cup develops, the latter process requiring about four days longer. The colour of the stipe remains unchanged throughout, viz. a pinkish buff at the top and clay colour at the base. The outer surface of the cup is clay coloured in both young and old stages, while the hymenial surface is clay coloured when young and sepia when old (Ridgway, Plate XXIX, 6). In length of stipe and diameter of cup the artificially produced apothecia agreed well with the natural ones already described.

Apothecia are formed only when the culture reaches a certain age of development and are confined to the thick dark brown or black



Text-fig. 4. Microconidia of *Lambertella* produced in culture.  
Camera lucida drawing.

pseudosclerotial crusts which develop over the surface of the culture. They appear after about seven weeks from the date of inoculation.

The average size of asci produced in culture was  $110 \times 8.7 \mu$ , i.e. they are somewhat larger than those naturally occurring. The size and appearance of the ascospores were essentially the same in both.

Light appears to be a factor of considerable importance in stimulating the formation of apothecia. This was suggested by the behaviour of the cultures during the first year after isolation. The mummies were collected in the autumn of 1931, and by the time artificial cultures were prepared it was already November. Throughout the winter cultures were set up on a variety of media at different times and exposed to diffused light on the laboratory bench near a window. No apothecia appeared, but from time to time an occasional stipe. In the following spring and summer, fully developed apothecia

appeared in abundance under the same treatment. The following experiment illustrates the effect of light more critically.

Cultures were set up on 2 per cent. malt agar in plates and tubes. Some of these were wrapped in black paper, others in white paper and the remainder in transparent (cellophane) paper and placed near a window. The appearance presented after about seven weeks was:

Cultures wrapped in cellophane, numerous mature apothecia.
"      "      white paper, numerous long stipes.
"      "      black paper, no fruiting structures.

This experiment was carried out three times with the same result.

A high degree of atmospheric humidity is necessary for formation of apothecia. This was shown by the following experiment.

Eight plate cultures on 2 per cent. malt agar were prepared, and after incubation for three weeks in the ordinary way at laboratory temperature were placed, after removal of the lids, as follows: four in a large container kept moist with water and four in a similar vessel containing a strong solution of calcium chloride. Only the former developed apothecia.

During the summer of 1933 it was noticed that when the temperature rose above 25° C. apothecia no longer developed, while those which were already present rapidly withered and disintegrated. Once the temperature again fell below 25° C. they began to appear again.

The composition of the medium is of some importance. In a comparative test of various media, apothecia were formed on the following:

Potato dextrose agar	{	200 gm. potato per litre	
	15	"  dextrose	"
Malt agar	20	"  malt	"
Prune agar	20	"  prunes	"
Coons's agar			
Oatmeal agar	50	"  oatmeal	"

these media being arranged in descending order of suitability. On potato extract agar (200 gm. potato per litre) and on Brown's A and Richards's agar no apothecia were formed. Apparently the development of apothecia is dependent upon the formation of pseudosclerotial crusts, and these do not appear on the media last mentioned.

The effect of acidity was tested by preparing starch peptone media with initial *pH* as follows: 2.2, 2.6, 3.0, 4.0, 4.4, 5.0, 5.4, 6.2 and 6.8. It was found that stipes first appeared in the culture of *pH* 4.4, then later at *pH* 4.0, and later still at *pH* 3.0, 5.0 and 5.4. So far no stipes have appeared outside the range *pH* 3.0-5.4.

## SECRETION OF ENZYMES

## I. Oxidising enzymes

In a previous section the tendency of *Lambertella* to produce a brown to black discolouration of the medium, especially on natural decoctions, has been noted. Later it will be shown that similar effects are produced on parasitised fruits. This behaviour suggested that oxidising enzymes might play a part, and for that reason the following determinations were carried out.

The two reagents used were guaiacum emulsion and pyrogallic acid prepared according to the recommendations of Wormald (11), as follows: To 10 gm. of gum guaiacum were added 100 c.c. of 95 per cent. alcohol, the mixture shaken at intervals over three days, and then filtered. The red-coloured filtrate was used as stock solution. The emulsion was prepared freshly for each test by shaking 5 c.c. of the tincture with 95 c.c. of distilled water, a white emulsion resulting. In carrying out the test, 1 c.c. of the liquid to be examined was added to 5 c.c. of the emulsion in a test tube. This method can be used to a certain extent quantitatively by noting the time required for the appearance of a blue colour of standard intensity.

The pyrogallic acid reagent was prepared freshly for each test, a 2 per cent. aqueous solution being used. In carrying out the tests 2 c.c. portions of the medium under examination were pipetted into test tubes and 5 c.c. of the acid added to each. A yellow coloration appeared in the presence of oxidising enzymes.

Controls were used throughout the tests by placing the tubes containing the culture solution in boiling water for twenty minutes before adding the reagent.

For comparative purposes cultures of *Lambertella*, *Monilia fructigena* and *Sclerotinia aestivalis* were tested in this respect. Each was grown in small flasks containing 30 c.c. of apple extract and incubated at 20° C. It was noted that after two days' growth *Lambertella* had produced a dark colour in the medium and that *Monilia* gave the same degree of darkening only after five days. On the other hand *S. aestivalis* gave no colour change. When the cultures were seven days' old, the liquid of each was filtered off and tested with guaiacum emulsion.

Table I gives the times required for certain standard colours to develop in the various tests.

From both sets of results it is clearly indicated that *Lambertella* is more active in excreting oxidising enzymes than is *M. fructigena* and that again the latter is more active than *S. aestivalis*. As the development of colour on media follows the same order, there are grounds for suggesting that oxidising enzymes are the active agents concerned.

Table I.

Fungus	Pale blue*	Caerulean blue*
<i>Lambertella</i>	10 mins.	45 mins.
<i>M. fructigena</i>	45 "	80 "
<i>S. aestivalis</i>	120 "	148 "
Fungus	Beryl blue*	Light methyl blue*
<i>Lambertella</i>	10 mins.	45 mins.
<i>M. fructigena</i>	45 "	115 "
<i>S. aestivalis</i>	115 "	115 "

\* As in Ridgway.

## 2. Pectinase

The capacity of *Lambertella* to attack apple fruits, to which reference will be made later, suggested that it is able to excrete the cell-wall dissolving enzyme, pectinase. Tests were carried out, and for purposes of comparison *Monilia fructigena* and *Sclerotinia aestivalis* were also examined. It should be noted that the parasitic vigour of these three fungi diminishes in the order *Monilia*, *Lambertella*, *Sclerotinia*.

Cultures were set up in tubes on sterilised turnip and apple plugs. After a certain time the juice was extracted and its activity tested on potato discs of standard thickness. The time required for loss of coherence of these discs to take place is in inverse ratio to the activity of the extracts. Also controls were set up in which boiled extracts were used.

In no case was the presence of enzyme detected in cultures of *S. aestivalis*. Table II gives the times required for decomposition of the standard discs in various extracts from turnip-plug cultures of *Lambertella* and *Monilia*.

Table II.

Age of culture	<i>Lambertella</i>	<i>Monilia fructigena</i>
10 days	570 mins.	120 mins.
17 "	225 "	40 "
24 "	170 "	35 "
31 "	90 "	30 "
38 "	90 "	30 "

Similar results were obtained with cultures on apple plugs. The controls were inactive in all cases.

Cultures of all three fungi likewise gave positive tests for the enzymes diastase, invertase and maltase.

## PATHOGENICITY

In carrying out inoculations of fruits, Granger and Horne's (3) method as somewhat improved by Vasudeva (10) was used. The most extensive tests were made with apple fruit, and in this connection a comparison was made of the rate of invasion by the three fungi,

*Lambertella Corni-maris*, *Monilia fructigena* and *Sclerotinia aestivalis*. To control the error due to variable resistance of different apples, both fungi in any comparison were inoculated into opposite sides of the same apple. Uninoculated but wounded controls were set up as usual, and reisolations from infected fruits were carried out.

Table III gives the average surface spread and weight of rotted tissue in a batch of four apples inoculated with *Lambertella* and *S. aestivalis* after ten days' incubation at 20° C.

Table III.

	<i>Lambertella</i>	<i>S. aestivalis</i>
Diameter of lesion (cm.)	4.5	2.7
Weight of rot (gm.)	15.2	3.0

Table IV gives a similar comparison of *Monilia fructigena* and *Lambertella* over a range of temperatures.

Table IV.

	10° C.		15° C.		20° C.	
	<i>M.</i>	<i>L.</i>	<i>M.</i>	<i>L.</i>	<i>M.</i>	<i>L.</i>
Diameter after 6 days (cm.)	3.2	1.8	4.0	2.2	6.5	2.3
Weight of rot , , , (gm.)	9.0	2.1	23.4	3.9	52.5	2.9

Tables III and IV show clearly that *Monilia fructigena* is a more active parasite of apple fruit than is *Lambertella*, which again is more active than *Sclerotinia aestivalis*.

Further inoculations showed that *Lambertella* attacks pears and plums both ripe and unripe, orange, lemon (Plate IV, fig. 5), quince, and such vegetables as turnip and parsnip. Potato and carrot were not attacked. Invasion of orange and lemon took place chiefly along the locular walls. Artificially inoculated plums (Plate IV, fig. 6), after being kept a few months, were shrunken and rubbery in texture. Brown at first, they finally become covered with an almost continuous layer of black pseudosclerotial crust-like material.

A firm brown rot is caused, especially in apples and pears (Plate IV, figs. 7 and 8). The rot gradually extends throughout the flesh, thoroughly absorbing it and forming a pseudosclerotium with the toughness and elasticity characteristic of the brown rot fungi, *Sclerotinia fructigena* and *S. fructicola*. These species, however, give a black pseudosclerotium, whereas that of *Lambertella* is brown. On the surfaces of fruits thus mummified, there may appear small white masses of hyphae, spherical to dome-shaped and closely resembling the immature pustules of *S. fructigena* on apple. (Plate IV, fig. 8, right). No spores are produced. The hyphal mass thickens and gradually darkens until dark sclerotoid bodies are scattered all over the surface of the mummifying fruit. These possess the power of

“creeping”—the fungus grows out from the edges of these bodies, forming a thin crust over much of the surface of the fruit. No conidial stage has been seen on infected fruits.

Inoculations of plum and apple blossoms in the spring of 1933 indicated that attack had taken place inasmuch as none of the inoculated flowers subsequently set fruit. Here the inoculum of mycelium with malt agar was laid inside the flower. Flowers in which malt agar only was used set fruit in the normal way. Unfortunately intermediate stages were not observed, so that while there is reason for thinking that the fungus attacked the blossom the experiment stands in need of confirmation.

A parallel series of wound inoculations into branches of apple, pear, cherry and plum gave negative results; all the wounds become callused over in due course. This was true both for inoculations of the current and the previous year's wood.

#### TAXONOMIC DISCUSSION

The present record appears to be the only one since von Höhnel described apothecia received from Lambert in Austria in 1917. Von Höhnel's collection is preserved in the Farlow Herbarium at Harvard and contains twenty-nine mummified fruits, one of which bears eleven apothecia. Examination of some of this material showed that it agreed in all points of taxonomic value with the fungus collected on apples and pears in 1931. From the accompanying notes it is clear than von Höhnel noted the change in colour of the spores from transparent when young to dark brown when mature. He gives a diagram of hyaline spores with rounded ends, measuring  $8 \times 4 \mu$ , and another of dark spores with more pointed ends, measuring  $8-12 \times 4 \mu$ . In another note the measurement of the asci is given as  $80 \times 6-8 \mu$ , but generally  $100 \times 8 \mu$  when they are mature. The full description (*loc. cit.*) is unaccompanied by figures.

Von Höhnel's record is listed by Strasser (9) and by Saccardo (8). The latter states that *Lambertella* “est *Sclerotinia phaeospora*”; von Höhnel describes his fungus as a “*Stromatinia* mit gefärbten Sporen”.

There are however two other records of a *Sclerotinia* with brown spores. In 1912 Sasaki discovered apothecia with brown spores arising from mummified apples in Japan. The fungus was described by Hori (6), who regarded the brown spores as sufficient justification for a new genus, *Phaeosclerotinia*, and named the fungus *P. nipponica*. Later (7) he apparently revised his opinion and altered the name to *Sclerotinia phaeospora*.

Hori examined *P. nipponica* in culture and showed that it had a *Monilia* stage. It was probably on this account that he subsequently transferred it to *Sclerotinia* as *S. phaeospora*. Von Höhnel does not

mention a *Monilia* stage, nor has such been found in the present case, even after extensive search. The Japanese fungus may thus prove to be distinct from that of von Höhnel. The point can be determined only by a careful comparison of the descriptions and material. It will be noted that, if the two fungi are identical, and if the name *Phaeosclerotinia nipponica* was properly published before 1918, then *Lambertella Corni-maris* von Höhnel becomes a synonym of *Sclerotinia phaeospora* Hori. Incidentally, the specific epithet *Corni-maris* is not a very happy one for a fungus which possesses a much wider range of hosts than the name indicates.

The second occurrence of a *Sclerotinia*-type of fungus with brown ascospores is in a collection of Bermudan fungi made by Prof. H. H. Whetzel in 1923-4 and now preserved in the Plant Pathological Herbarium at Cornell University. This material has not been fully described and so far is provisionally labelled as *Sclerotinia* sp.

According to Whetzel\* *Lambertella Corni-maris* is a typical *Ciboria*, both in its general characteristics and its cultural behaviour. He considers that, even among the Discomycetes, the colour of the ascospores alone is not sufficient to justify generic rank. On the other hand, von Höhnel evidently thought that spore colour was important. Variation in spore colour within a genus is common among the Pyrenomycetes, but is so rare in the Discomycetes as to constitute a striking feature. Certainly the general view of mycologists in England with whom the matter was discussed was that von Höhnel was justified in proposing his new genus.

Prof. Whetzel's suggestion that *Lambertella Corni-maris* is a species of *Ciboria* is not at present acceptable. The taxonomy and nomenclature of the Sclerotiniae is in process of revision, and it is hoped that before long Prof. Whetzel will publish characters indicating at least the generic concepts held. The line of demarcation between *Ciboria* and *Sclerotinia* is difficult to determine by consulting the existing definitions and descriptions of these overloaded genera.

Finally, Dr E. E. Honey\* in an unpublished monograph proposes to include the Japanese fungus under the genus *Monilinia* on the ground that the colour of the ascospore does not prevent the fungus from being a good representative of the "Monilioid Sclerotinias." The status of *Monilinia* would come up for consideration in the present connection if it were shown that *Lambertella* possessed a *Monilia* stage.

In conclusion, while the authors agree that the validity of von Höhnel's genus *Lambertella* is somewhat in doubt, they suggest that the name *Lambertella Corni-maris* von Höhnel be retained until a strict examination of all the relevant material has been made.

\* Private communication.

The authors are indebted to the following gentlemen for facilities in their various institutions: Dr E. J. Butler and Mr S. P. Wiltshire of the Imperial Mycological Institute, London; Mr J. Ramsbottom, Department of Botany, British Museum (Nat. Hist.); Prof. W. H. Weston, Botanical Department, and Mrs Riddle, Farlow Herbarium, Harvard University; Prof. H. H. Whetzel, Cornell University; and finally Prof. W. Brown, Imperial College of Science and Technology, London, in whose laboratory all the cultural work was carried out.

#### SUMMARY

1. A Discomycete with brown ascospores was collected from mummified apples in Switzerland and from mummified pears in Germany in August 1931.
2. Taxonomic details are presented to show that it is identical with one collected from fruits of *Cornus mas* in Austria in 1917.
3. The fungus grows on a large variety of media. A thick dark brown or black pseudosclerotial crust develops over the surface of the culture on most of the media. The optimum  $\text{pH}$  for growth is at a point of relatively high acidity, viz. near  $\text{pH}$  4.4; and growth occurs over a wide range of  $\text{pH}$ , viz. from 1.6 to 8.3.
4. The existence of an imperfect stage is doubtful, whereas apothecia with ascospores are produced on a variety of media under suitable conditions of light, humidity, temperature and acidity. They are confined to the black pseudosclerotial crusts.
5. The fungus is very active in excreting oxidising enzymes as well as pectinase.
6. Under laboratory conditions the fungus attacks a variety of fruits and vegetables (apple, pear, plum, quince, orange, lemon, turnip and parsnip). Inoculations of apple and plum blossoms appeared to give positive results, whereas no attack resulted in inoculations of young wood of apple, pear, cherry and plum.
7. The nomenclature of the fungus is discussed and the conclusion reached that for the present the name for the organism must be *Lambertella Corni-maris* von Höhnel.

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## EXPLANATION OF PLATE IV

Fig. 1. Apothecia from mummified apple found at Viège, Switzerland.  $\times 1.8$  approx. Phot. S. P. Wiltshire.

Fig. 2. Mummified pear bearing 21 apothecia. Photographed *in situ*, Baden-Baden, August 1931. Nat. size.

Fig. 3. Detailed view of apothecia on mummified pear. Nat. size.

Fig. 4. Apothecia produced on 2 per cent. malt agar culture kept in daylight.  $\times 0.8$  approx.

Fig. 5. Infected orange (l.) and lemon (r.).

Fig. 6. Branch of plum bearing infected fruits.

Fig. 7. Inoculated pears, after ten days at  $20^{\circ}\text{C}$ .

Fig. 8. Inoculated apples.



Fig. 1

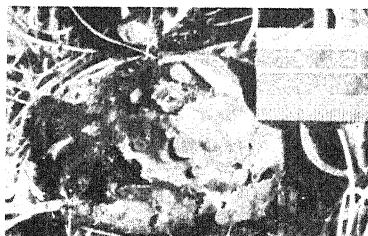


Fig. 2



Fig. 3

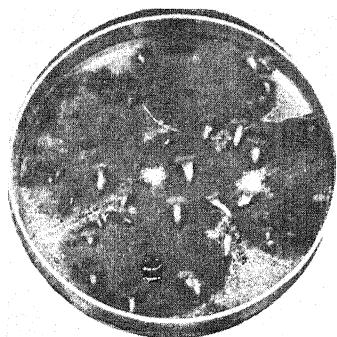


Fig. 4

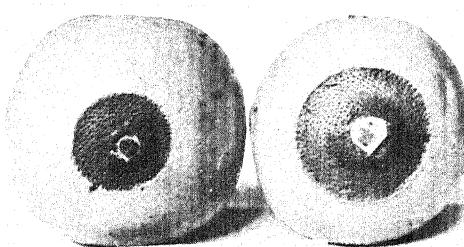


Fig. 5

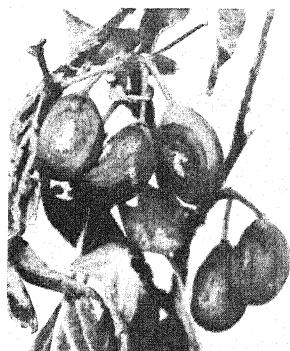


Fig. 6

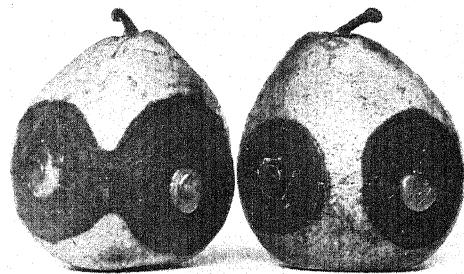
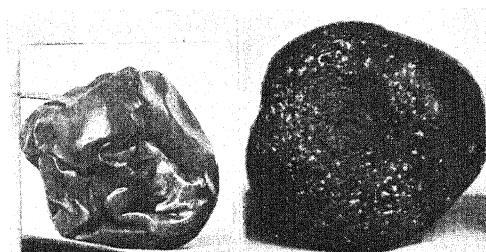


Fig. 7





## NEUROSPORA IN BRITAIN

By J. RAMSBOTTOM AND F. L. STEPHENS

(With Plates V-VII)

“*MONILIA SITOPHILA* (MONT.) SACC.” as a collective species has become one of the best known and most important fungi owing to the work of Shear and Dodge (1927) and Dodge and his pupils since that date. Their discovery of the perfect stage for which they instituted a new genus, *Neurospora*, has had considerable influence on mycological thought. The purpose of the present paper is to record two species of *Neurospora* for this country but it seems advisable to note certain points which were studied in making the identifications.

The fungus is called “red bread mold” by Shear and Dodge because of its frequency as a bakery pest. In 1842 the French Minister of War appointed a commission to investigate the cause of an infestation of Army bakeries. Léveillé (1843) named the fungus *Oidium aurantiacum* and the same year Montagne called it *Penicillium sitophilum*; it was transferred to *Monilia* by Saccardo (1881). Outbreaks of the fungus have also been recorded from Germany, Italy, and U.S.A.; we know of no such trouble in the British Isles.\*

Petch (1931) has given an account of the recorded occurrences of *Monilia sitophila* in this country. These are:

On rotting seed after the burning down of an oil mill, King’s Lynn, 1899. C. B. Plowright.

On charred grain after a mill-fire, Grantchester, 1928-9. F. T. Brooks.

On burnt trees, Bawsey, near King’s Lynn, 1929. T. Petch.

Petch says “It is curious that there are no previous records of this fungus in Great Britain. One would have expected that it would have occurred on charred gorse after heathfires.” One of our specimens is from such a habitat. It was found while demonstrating the conidial stages of *Daldinia concentrica* at a fungus foray of the Plumstead and Woolwich Natural History Society at Woolwich, on October 2nd, 1933. There had been a fire during the summer and

\* We have since learned from the Plant Pathological Laboratory, Harpenden, that the fungus occurred in a bakery in the Irish Free State in August, 1933. Dr E. A. Fisher informed Dr G. H. Pethybridge that “he believes that outbreaks of this fungus in bakeries in England are rather uncommon.” Mr C. G. C. Chesters has kindly sent us cultures which he isolated from dough sent to him from a bakehouse “several years ago”: the material contained ascospores.

the scorched stems of *Ulex* showed a salmon-pink growth which was obviously not *Pyronema confluens*. It is not unlikely that the fungus is fairly common in such conditions, but so far we have no confirmation of this belief.

We have also obtained a culture from the National Collection of Type Cultures. It had been sent to the Lister Institute by Mr G. Smith who informs us that he obtained it about three years ago when he was plating out hundreds of samples of cotton yarns. "It occurred occasionally as a single colony on one plate of a series and was most probably just a chance infection."

While the first fungus was being investigated Mr W. H. Wilkins found a second form growing in enormous quantity on the ends of beech battens which were being kiln dried in a timber yard at Chichester.

The apparent rarity of the fungus is surprising when its extensive distribution in America is considered, for there the fungus (*sens. lat.*) infects sugar-cane bagasse and silage and causes a storage rot of fruits especially strawberries, raspberries and apples. It is also "well-known to laboratory workers in mycology and pathology as a contamination in cultures of other organisms."

There is no doubt that the fungus found commonly on charred material in the tropics and usually called *Monilia carbonaria* Cooke belongs to the same group of species; Cooke's species was described from burnt wood and stems in New Zealand. "People's utmost attention was directed towards a remarkable reddish yellow fungus which has grown up luxuriantly on the bark of burnt or half-burnt trees after a few days of the terrible fire of Tokyo on September 1, 1923. The fungus was found to belong always to the same species, though a number of Coniferous as well as broad-leaved trees were over-grown with it. It appears externally just like some wild yeast which very commonly is found living on the exudation of some trees or on some organic substances, but under the microscope it reveals itself evidently to be a certain species of *Monilia*" (Kitazima, 1925).

Shear and Dodge give the synonymy of *Monilia sitophila* (Mont.) Sacc. as: *Penicillium sitophilum* Mont.; *Oidium aurantiacum* Lév.; *Monilia Martii* Ell. & Sacc.; *Oospora aurantiaca* (Lév.) Herter; *Monilia aurantiaca* (Lév.) Herter non Peck and Saccardo; *Oidium Lupuli* Matth. & Lott.; *Oospora Lupuli* (Matth. & Lott) Lindau; *Monilia aurea* Kitazima non Gmelin; and they query *Monilia carbonaria* Cooke.

The inclusion of *Oidium Lupuli*\* is noteworthy because it was first described from spent hops in this country. The original account reads: "*Oidium Lupuli* is an excellent example of a mould resembling *Oidium lactis* in its mode of growth; it is occasionally met with on spent hops,

\* *Monilia Lupuli* Mass. apud Grove in *J. Econ. Biol.* vi (1911), 412.

on which it forms a reddish yellow or salmon-coloured dust, which on microscopical examination, is found to consist of branching cells, merging like *Mucor Racemosus* into spherical cells, some of which have all the appearance of budding. Many of the spherical cells and the branching pieces display an orange-pink colour, which seems to permeate the protoplasm. For a purely aerobian form, the mode of reproduction is decidedly interesting" (1889, pp. 86-7). This is the same fungus as *Oidium aurantium* Cooke issued in *Fungi Britannica Exsiccati* No. 448 and also in Rabenhorst's *Fungi Exs.* No. 1579 and described in *Grevillea*, 1 (1872), 21: "Oidium aurantium Cooke. 'Orange oidium.' Forming dense, irregular, effused, bright orange tufts, sometimes several inches in length. Hyphasma creeping, branched, robust, septate, surmounted by simple or branched moniliform threads, which break up into subglobose or elliptical spores; endochrome granular.—Cooke exs. No. 488, on spent hops. Burton-on Trent. August 1871 (Edwin Brown, Esq.)."

This species appears in Saccardo, *Sylloge Fungorum*, iv (1886), 22 as *Oospora aurantia* (Cke.) Sacc. & Vogl (cf. Massee, *Fungus Flora*, III (1893), 280).

According to information we have received this fungus is not infrequent in this country. It was noticed on hop manure exhibited at the Chelsea Flower Show in 1930\* and has been kept in culture since. Shear and Dodge are correct in assigning it to *Monilia sitophila* †.

The fungus which was gathered on burnt *Ulex* was cultured. After a few days perithecia formed and on examination were found to agree exactly with the description of *Neurospora tetrasperma* Shear & Dodge. This was a matter of great surprise for this fungus appears to have been known previously only from Surinam, Dutch Guiana, "and a few places as yet" (Dodge, 1930).

***Neurospora* Shear & Dodge in *J. agric. Res.* xxxiv  
(1927), 1025**

"Perithecia gregarious or scattered, smooth or with loose hairs, subcoriaceous to subcarbonous; ostiole papillate or short rostrate, perithecial cavity lysigenic, filled at first with parallel, septate hyphae (paraphyses?) which begin to collapse and disappear as soon as the young asci start and are entirely gone when the asci are full grown; spores hyaline to yellowish-brown at first, becoming black or greenish black when mature, continuous, longitudinally ribbed. Conidial stage of the *Monilia sitophila* type.

The perithecia are either superficial or embedded when grown on agar media; when superficial they usually show a loose growth of

\* Also at the Autumn Show, Crystal Palace, Sept. 1934.

† The combination *Candida sitophila* is used by Jaczewski in his *Elements de la Mycologie*, p. 196 (1933).

weak hyphae on the surface. The crowded septate hyphae which fill the perithecial cavity at the time the asci start are doubtfully described as paraphyses. They disappear so soon that they would not be observed except in very young perithecia."

*Neurospora tetrasperma* Shear & Dodge, *tom. cit.*

p. 1027

"Conidial stage (*Monilia tetrasperma* nom. nov.): On corn-meal agar in tubes very scanty whitish growth of mycelia about the upper edge of the agar slant; conidial tufts usually small and scanty, pale salmon; sporogenous hyphae irregularly ascending, septate, dichotomously branched; conidia catenulate, connected by a narrow isthmus when mature, globose to subglobose, smooth, nearly hyaline or pale salmon in mass,  $8-11\mu$  in diameter, mostly  $8-9\mu$ .

Perithecial stage: Perithecia gregarious or scattered, superficial or immersed when grown on agar media, smooth or loosely and sparsely soft hairy when superficial, yellowish when young, becoming dark brown to black;  $250-300\mu$  in diameter; wall medium thick, subcoriaceous; ostiole obtuse, papillate; paraphyses (?) crowded, septate, collapsing and disappearing as soon as the asci appear; ascospores uniseriate or somewhat overlapping, oblong-elliptical with about 20 longitudinal, sometimes branched ridges, olivaceous at first, becoming dark brown to black,  $29-35 \times 14-16\mu$ , mostly  $30-31 \times 15\mu$ . This species is homothallic." Collected on charred furze stems in quantity, Bostall Heath, Woolwich, October 1933 (J.R.).

In our cultures conidia were rather sparsely developed. The majority of asci contain four spores c.  $35 \times 17\mu$ ; some have six or five spores and occasionally three. The small spores vary from  $24-31 \times 4\mu$ , the larger ones may be over  $40\mu$  long. We have compared the fungus with a culture obtained from Dr B. Colson (cf. *Ann. Bot.* XLVIII (1934), 211-25) subcultured from one sent to her by Drs Shear and Dodge. The two are identical.

The fungus sent to us in culture by Mr Wilkins agrees with the description given by Shear and Dodge for their *Neurospora sitophila*. There was a certain relief felt when this was realised for it would have been a little unfortunate to have a conidial stage recorded for this country as *Monilia sitophila* and only *Neurospora tetrasperma* as a perfect stage. Mr Wilkins's discovery conveniently disposes of any questioning of Shear and Dodge's statement about *M. sitophila*. "Whether this species is identical with Montagne's fungus it is impossible to determine at present, as the ascospore stage of his plant was not found. This is the common red bread mold of Europe and America and presumably Montagne's species; for practical purposes, therefore, this name may be adopted." The specific epithet of the perfect stage takes precedence over that of the conidial stage but it would be some-

what incongruous to have it open to question whether *Monilia sitophila* was really the conidial stage of *Neurospora sitophila* with a possible upsetting of the nomenclature adopted by Shear and Dodge, and the usual complications rendered a little ludicrous.

***Neurospora sitophila* Shear & Dodge, tom. cit. p. 1026**

“Conidial stage (*Monilia sitophila* Mont.): On corn-meal agar tufted or irregularly pulvinate at first, soon becoming effuse and fluffy; conidial masses varying from pale salmon to orange color; mycelium hyaline, creeping, septate; sporogenous hyphae irregularly ascending, septate, dichotomously branched; conidia catenulate, connected by a narrow isthmus when mature, globose to subglobose, smooth, pale salmon to orange in mass, 10 to 12  $\mu$  diameter, mostly 10 to 11  $\mu$ .

Perithecial stage: Perithecia gregarious or scattered, superficial or immersed on agar media, smooth or loosely soft, hairy, brown to black subcoriaceous, 200 to 300  $\mu$  diameter; ostiole papillate; asci cylindrical, short stipitate, apex with a thickened gelatinous ring, 8-spored, 140–160  $\times$  12–14  $\mu$ ; paraphyses (?) crowded, multiseptate, filling the peritheciun at first, collapsing and disappearing as the asci develop; ascospores overlapping uniseriate, elliptical, with 16 to 17 sometimes branched longitudinal ribs, olivaceous becoming dark greenish black, 20–26  $\times$  10–15  $\mu$ , mostly 23–25  $\times$  13–15  $\mu$ .”

Our cultures produced large quantities of conidia, especially at the top of the culture tube or at the edge of the Petri dish.

The main interest in *Neurospora* is in the occurrence of both homothallism and heterothallism which are connected with the nuclear condition of the ascospores. Shear and Dodge found that *N. tetrasperma* was homothallic and *N. sitophila* was heterothallic. It was found that small spores which occur with some frequency in the asci of *N. tetrasperma* gave strains which did not produce perithecia in the ordinary way but only when mated. Dodge (1927), showed that *N. tetrasperma* had ascospores which were normally binucleate but that the small spores were uninucleate like the spores of *N. sitophila*, thus finding a nuclear explanation of the presence of both homothallism and heterothallism in the one species.

The conidial stage of *N. tetrasperma* gathered on burnt gorse was cultured on Sabouraud's maltose and glucose media and on potato agar. Hyphae and conidia grew very rapidly and numerous well-formed perithecia were formed in about seven days being particularly abundant on the potato agar. Cultures from single ascospores were obtained by placing a few drops of a dilute spore suspension on to agar in a Petri dish. The spores were examined under a microscope and rings made round those which were well isolated. These were then transferred to fresh Petri dishes. The majority of the cultures were homothallic producing perithecia in abundance.

Heterothallic strains were obtained by plating out very small spores. Sterile "sclerotia" developed but no perithecia occurred unless two opposite strains were mated. Strains which were labelled A, X and Y were paired. A plus X and X plus Y always produced perithecia, but A plus Y was invariably sterile (Pl. VI, figs. 1-3). Perithecia usually occurred on one half of the dish only; "sclerotia" appear everywhere.

From the culture sent by Mr Wilkins ascospore cultures were made. These when grown singly produced "sclerotia" but no perithecia. From a series of strains those labelled S, Q and R were mated: S plus Q gave fertile perithecia, S plus R gave fertile perithecia, R plus Q gave "sclerotia" only (Pl. VII).

In both *N. tetrasperma* and *N. sitophila* the sclerotia arise in the same way as the fertile perithecia. Coiled multinucleate hyphae (archicarps) are produced in abundance. These are quickly surrounded by large numbers of intricately woven sheathing hyphae. No antheridia are formed. The "sclerotia" or sterile perithecia usually attain a diameter of about  $100\mu$  but occasionally may be almost as large as the perithecia (Pl. V, figs. 7 and 10).

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#### EXPLANATION OF PLATES V-VII

##### PLATE V

###### *Neurospora tetrasperma*

Figs. 1-5. Developmental stages of archicarps.  
 Fig. 6. Conidia.  
 Fig. 7. Sclerotium.

###### *N. sitophila*

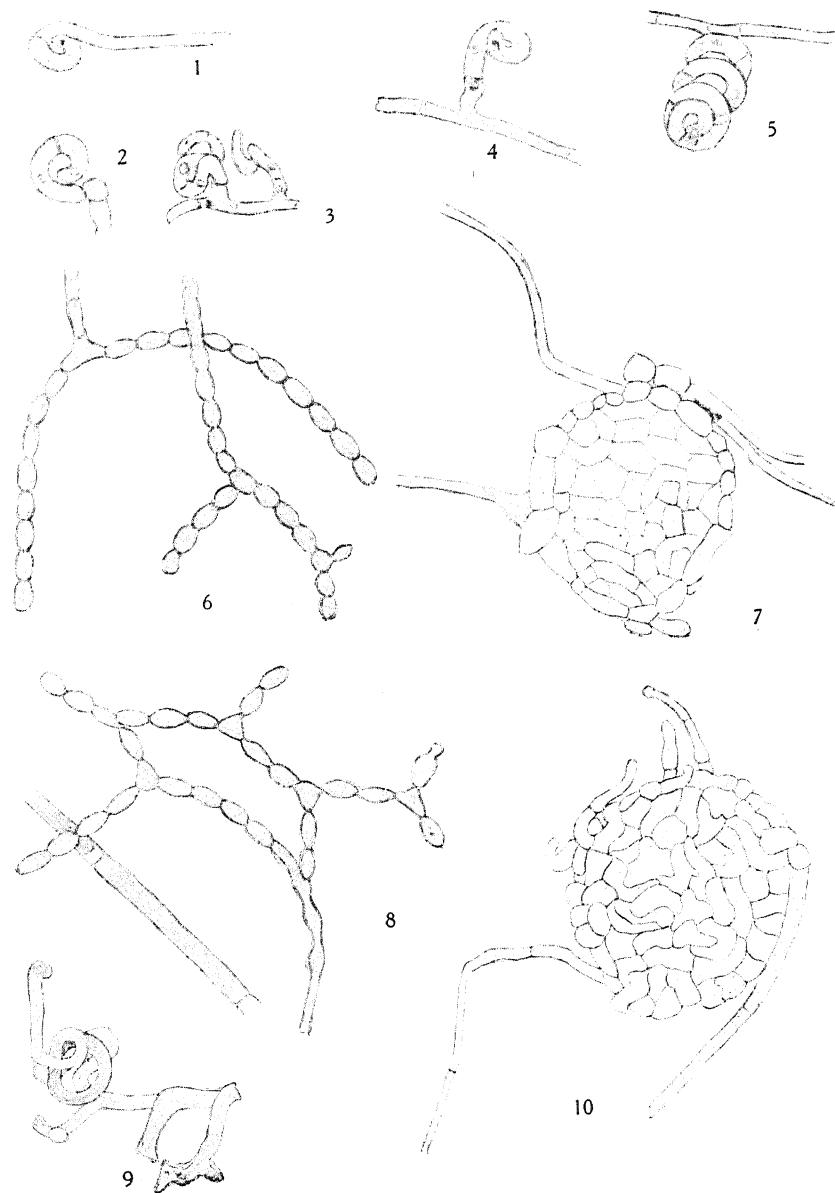
Fig. 8. Conidia.  
 Fig. 9. Archicarp.  
 Fig. 10. Sclerotium.

##### PLATE VI

###### *N. tetrasperma*. Strains X and A, X and Y, Y and A.

##### PLATE VII

###### *N. sitophila*. Strains S and R, R and Q, S and Q.





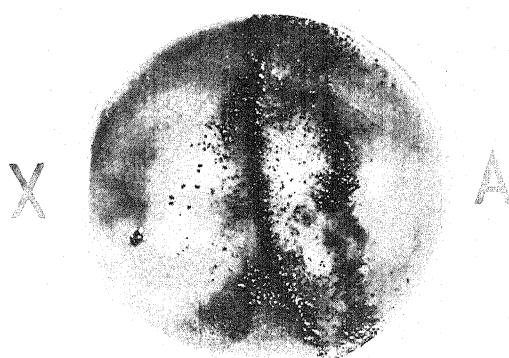


Fig. 1

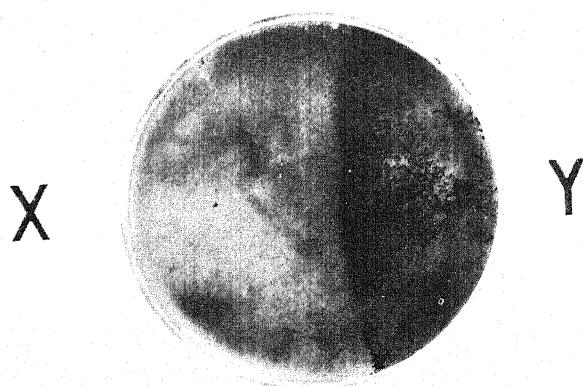
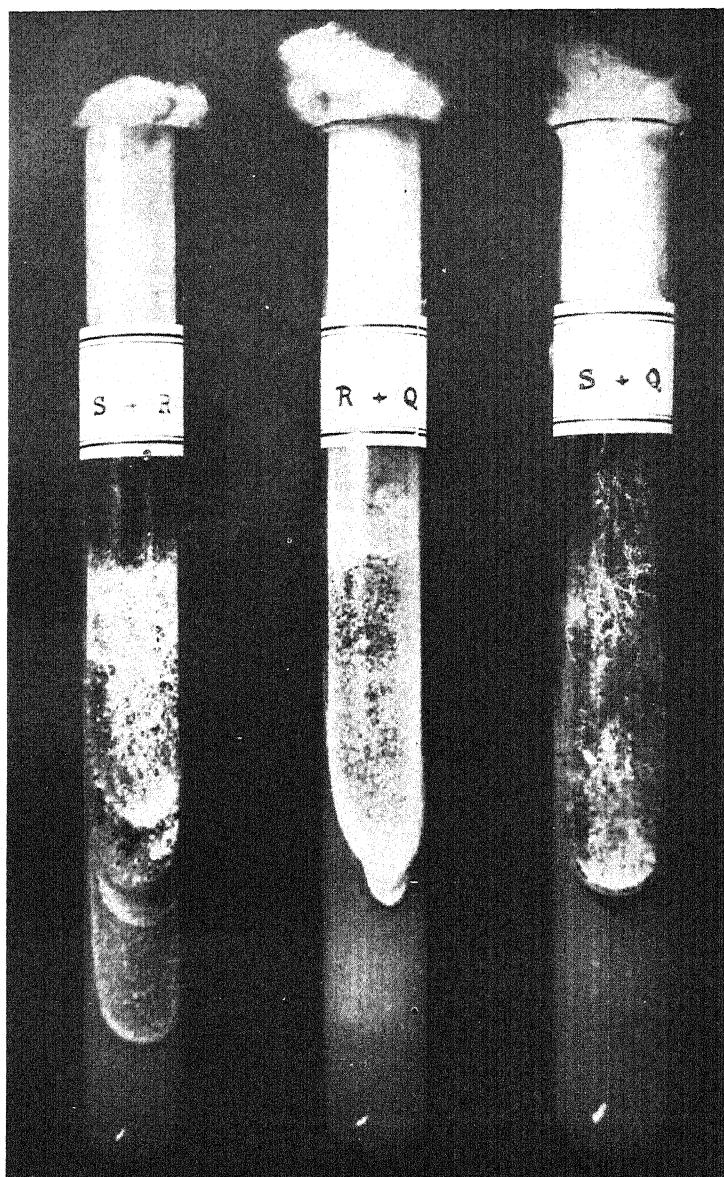
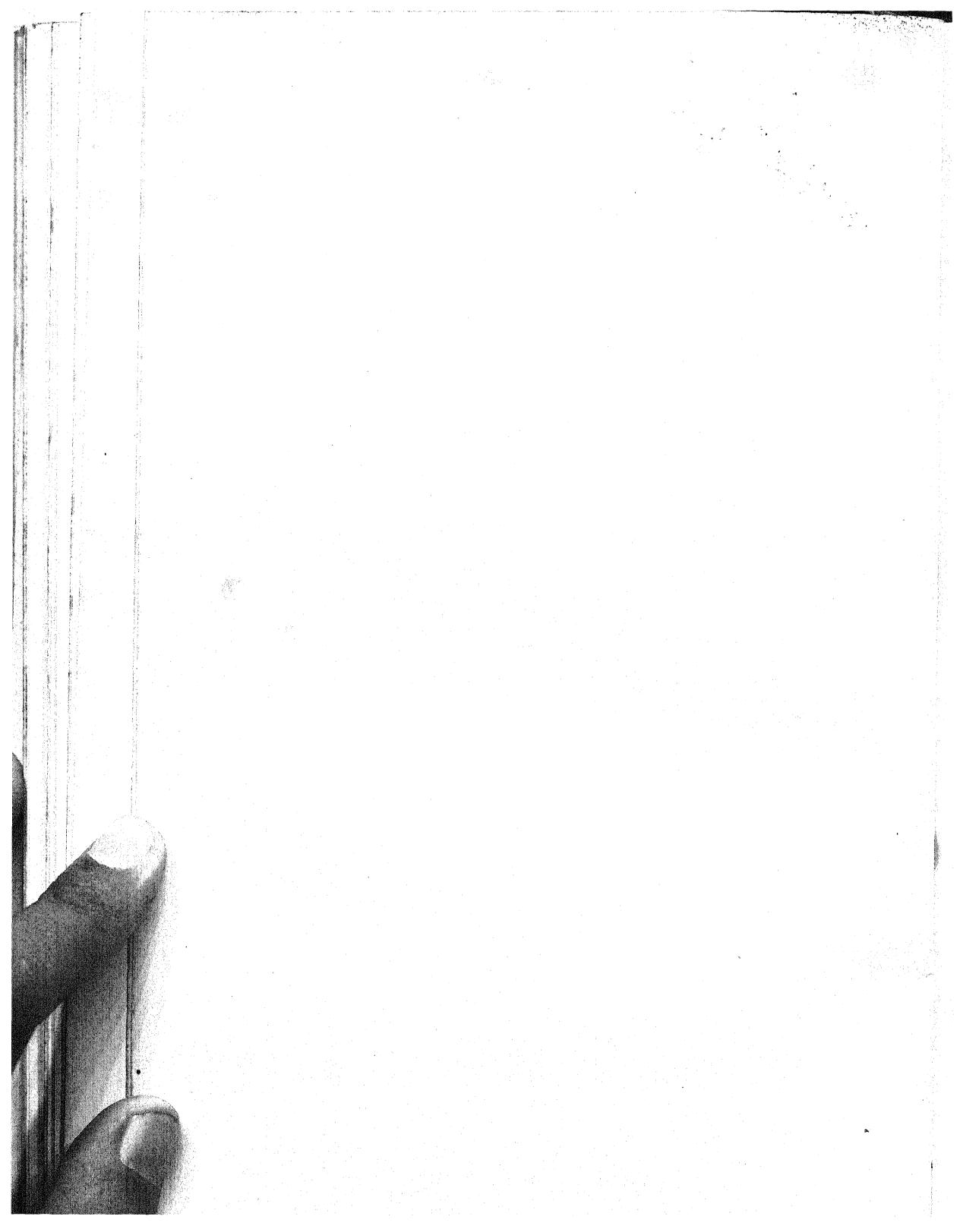


Fig. 2









## OBSERVATIONS ON SOME BRITISH WATER MOULDS (SAPROLEGNIALES AND BLASTOCLADIALES)

BY EVELYN J. FORBES

(*Department of Botany, Victoria University, Manchester*)

(With Plates VIII-X and 2 Text-figures)

### INTRODUCTION

THE first attempt to prepare a complete list of British aquatic fungi appears to be due to Massee<sup>(20)</sup>, who recorded eleven species of Saprolegniaceae. Ramsbottom<sup>(25)</sup> published a new list containing seventeen species of Saprolegniaceae and Leptomitaceae, and Barnes and Melville<sup>(1)</sup> added nine more species to the records. Sparrow reported the occurrence of *Rhipidium*, *Blastocladia* and *Sapromyces* in a paper read to the British Mycological Society in November 1932, and in a paper read to the British Association at Leicester, in 1933, Barnes recorded *Rhipidium europaeum* and *Sapromyces Reinschii* from another locality. Subsequent to that meeting, Cook and Forbes<sup>(7)</sup> published a preliminary account of their findings near Bristol, listing the present twenty-two species, of which fourteen were thought to be new records for this country.

Von Minden<sup>(21)</sup> and Petersen<sup>(24)</sup> have investigated systematically the aquatic fungi of Germany and Denmark. In America, Coker<sup>(3)</sup>, and his co-workers<sup>(4, 5, 6, 12)</sup>, during twenty years of investigation at the University of North Carolina, have perfected a technique for dealing with these fungi, and have found many new species, as well as many of the species described by earlier workers. These methods have now been applied with considerable success in an investigation of the water moulds of the Bristol district.

### METHODS

It is well known<sup>(13, 18, 23)</sup> that aquatic fungi are very susceptible to changes in the conditions of their environment, and that such changes may lead to variation even in those characters which have been regarded as constant and of value in classification. Consequently, in the work now to be described, the same substratum has been used throughout, and, as far as possible, the cultures have been kept under identical conditions.

The methods recommended by Couch (8) have been used in collecting and culturing the fungi.

#### *Rough cultures and preliminary measures*

Most natural waters seem to contain aquatic fungi. Such waters, brought into the laboratory in stoppered bottles, placed in crystallising dishes with loosely fitting covers and baited with halves of boiled hemp seeds, usually yield a visible mycelial growth in a few days. After washing with sterile distilled water, and transferring to pots of distilled water—preferably sterile—the mycelium on the hemp seed develops sporangia in a few days and sexual organs after a week or two; identification of the fungus is now possible.

#### *Pure cultures*

A piece of hemp seed may bear mycelia of more than one species. These may be identified provisionally, but pure cultures are necessary for the study of a complete life history. Pure cultures are obtained from single hyphae bearing sporangia or oogonia, teased out under the binocular microscope and transferred to plates of malt agar or of corn-meal agar. The mycelium is freed from bacteria by subculturing. Frequently, the fungi do not fruit on agar, and a portion of the mycelium must be transferred to distilled water in order to obtain the reproductive organs.

#### *Special culture methods*

Species of such genera as *Rhipidium* and *Blastocladia*, which have a differentiated basal segment attached to the substratum by rhizoids need special treatment. Such species do not grow on hemp seed but they develop well on fruits of rose. The fruits are placed in cylinders of perforated zinc moored by a wire and left in the water for three or four weeks. The fruits are then removed and placed in distilled water. The fungi develop as whitish pustules.

These forms cannot be transferred to other substrata, and pure cultures have not been obtained. Usually, however, a pustule contains only one species. Bacterial contamination is heavy and it is essential to keep these fungi at low temperatures (4–8° C.) if a satisfactory condition is to be maintained. The fruits must be washed frequently during the period of cultivation.

*Pythiomorpha*, although filamentous, also needs special treatment. It is not found on hempseed, but appears when grapes are used as bait; it has also been found on slices of apple, and twice on dead twigs. When grown on grapes, the fungus is treated in the same way as *Rhipidium*; pure cultures may be obtained on malt agar.

Collections were made during the period September to March, with the exception that *Brevilegnia* was found in August. Although the records refer only to those months, clear evidence of periodicity was shown by the work of Miss G. E. Allen, to whom I am indebted for a supply of the rough material which served as a starting point for the preparation of cultures used for the identification and description of many of the species. Miss Allen made regular collections in the neighbourhood of Bristol, and found that the species occurred in greatest abundance in January.

#### SYSTEMATIC

The classification used by Fitzpatrick<sup>(11)</sup> has been followed, with the exception that Petersen's<sup>(24)</sup> family, Pythiomorphaceae, has been retained, since a study of the reproductive organs of *Pythiomorpha* shows that Fitzpatrick was not justified in placing this fungus in the genus *Phytophthora*. Almost without exception, it has been found possible to accept the genera and species as they have been defined by Coker<sup>(3)</sup> and by Kanouse<sup>(15, 16, 17)</sup>.

In the record which follows, the species of each genus are divided into two groups:

- (a) Species already recorded in this country.
- (b) Species found for the first time in this country during the present investigation.

Full diagnoses are not given for the species of group A, but observations not agreeing with previous statements are recorded. The species of group B are fully described and the points in which there are differences from older descriptions are noted. Species of either group which were adequately figured by Coker<sup>(3)</sup> Kanouse<sup>(15, 16, 17)</sup> or in any other readily accessible account are not figured here, but references are given to the appropriate figures.

#### SAPROLEGNIACEAE

Genus *Saprolegnia* Nees v. Esenbeck (1823)

- (a) Species already recorded in this country

1. *Saprolegnia ferax* (Gruithuisen) Kützing, *Phyc. Generalis* (1843) (*Achlya prolifera*, Prings. in *Nova Acta C.L.C.N.C.* xxiii (1851), 395; *Saprolegnia dioica* Prings. in *Jb. wiss. Bot.* ii (1860), 206; *S. Thureti* de Bary, *Beitr. Morph. u. Phys. d. Pilze*, iv (1881), 102; *S. bodanica* Maurizio in *Jb. wiss. Bot.* xxix (1896), 107; *S. esorina* Maurizio in *tom. cit. p. 82*).

Figures: Coker, 1923, Pl. 11.

Found thirty times near Bristol from December to March.

*Saprolegnia mixta* de Bary in *Bot. Z.* xli (1883), 38.

Found three times near Bristol in November.

*Saprolegnia ferax* usually has antheridia on less than 10 per cent. of the oogonia, whereas *S. mixta* has antheridia on about 50 per cent. of the oogonia. *S. mixta* has been described by many authors since de Bary, and most have commented on the difficulty of regarding *S. ferax* and *S. mixta* as distinct species. The production of antheridia by *S. ferax* is a very variable character, and the same culture may at one time resemble *S. ferax* and at another be indistinguishable from *S. mixta* (Davis (9), Coker (3)).

It appears that *S. mixta* de Bary is really a growth form of *S. ferax* (Gruith.) Kütz., which is an extremely variable species under different environmental conditions. Some material without antheridia was obtained in the collections near Bristol, and other material had oogonia with 50 per cent. antheridia or more. No special factor seemed to be responsible for this variation.

The variability of this species extends to its growth habit and to other features. Von Minden (21) described two forms of *S. Thureti* (*S. ferax* (Gruith.) Kütz.), differing in the following points:

(i) Oogonia terminal, or often on long bent stalks, typically spherical, very rarely cylindrical.

(ii) Oogonia mostly on the ends of very short lateral branches, in regular racemose arrangement; many of the large oogonia, containing numerous eggs, cylindrical in empty sporangia.

The form described by Fischer (10) resembled the second of von Minden's forms, as did also in many respects those of Humphrey (14) and Coker (3). Form (ii) was the more common form found around Bristol, the racemose arrangement of oogonia and the frequent occurrence of cylindrical oogonia being very noticeable. These cultures were usually examined before they were more than a month old. In two experiments, cultures with the appearance of form (ii) were kept in distilled water for three or four months, and by the end of this time the character of the material had changed greatly. Cylindrical oogonia were no longer found, and the oogonia present were borne on side branches that were much longer than those of the former racemose arrangement. As the cylindrical form of the oogonia is due to their origin within old empty sporangia, it is to be expected that old cultures would cease to form such oogonia, since the hyphae have grown beyond the region where sporangia were produced. Young cultures contained oogonia on long and on short stalks, and there was no known reason for this variation. It seems probable that the two forms are not really distinct, and that they merge into one another.

A few young cultures however produced form (i) of von Minden.

(b) Species new to this country

2. *Saprolegnia monoica* Pringsh. in *Jb. wiss. Bot.* I (1858), 284 (*Diplanes saprolegnioides* Leitgeb, in *Jb. wiss. Bot.* VII (1869), 357, ? *Achlya intermedia* Bail in *Amtl. Ber. 35te Versamml. Deutsch. Naturf. n. Aerzte in Königsberg*, 1860, *Saprolegnia semidioica* Peters. in *Ann. Myc.* VIII (1910), 494).

Figure: Petersen, 1910, fig. I, p. 520.

Found four times near Bristol in January and February.

*Diagnosis.* Growth (on hempseed), up to 1 cm. long. *Hyphae* up to  $100\mu$  broad at the base. *Sporangia* and *spores* as usual in the genus; secondary sporangia very numerous and markedly constricted at intervals by mouths of earlier sporangia. *Oogonia* borne racemously on short, straight or bent stalks, spherical, with conspicuously pitted walls, smooth,  $60-110\mu$  diameter, usually  $70-90\mu$ ; basal wall frequently protruding into the oogonium. *Oospores* 6-22 per oogonium, usually 10 or more,  $19-24\mu$  diameter, mostly  $21\mu$ , centric. *Antheridia* clavate, androgynous, on all the oogonia, arising from the main hypha or from the oogonial stalk; antheridial stalks branched and often supplying more than one oogonium.

*Saprolegnia monoica* resembles *S. ferax* very closely in everything except the percentage of antheridia; Coker(3), however, by using suitable nutrient media, showed that the percentage of antheridia in *S. ferax* may be made to vary from 1 to 98. It is difficult to understand how a form of *S. ferax* with antheridia on nearly all the oogonia could be distinguished from *S. monoica* as found near Bristol.

It has been shown that, owing to the variability of the percentage of antheridia, it is not possible to separate *S. ferax* and *S. mixta* as good species. It now seems possible that the very variable *S. ferax* may include among its growth forms one which is indistinguishable from *S. monoica*; if that is so, *S. ferax* and *S. monoica* cannot be regarded as distinct species. An illuminating fact is that while *S. ferax* was most abundant in the collections made from September to November, *S. monoica*, which did not appear until November, became the more frequent in the later months. It seems possible that there are two growth forms whose appearance is controlled by some seasonal factor, such as temperature.

In these fungi a species seems to consist of a number of forms whose features vary over a wide range, merging into one another and often completely overlapping (cf. *Achlya de Baryana*). Such comprehensive species seem to be the smallest units with constant distinguishing characters into which these fungi can be divided. The forms within a species show definite tendencies which they preserve fairly constantly under normal conditions, but they are not true species, since one

form may be induced to assume the characters of another by variations in the nutrition (Klebs (19), Horn (13), Kauffman (18), and other authors). It therefore seems possible that *S. ferax*, *S. mixta* and *S. monoica* may in the future come to be regarded as forms of one species, exhibiting different tendencies, as shown in *forma ferax* (antheridia on 0-10 per cent. of the oogonia), *f. mixta* (antheridia on 50 per cent. of the oogonia) and *f. monoica* (antheridia on 100 per cent. of the oogonia).

2a. *Saprolegnia monoica* Pringsh. var. *glomerata* Tiesenhausen in *Arch. Hydrobiol. Plankt.* vii (1912), 261.

Figures: Coker, 1923, Pl. 13.

Found five times near Bristol from January to March.

*Diagnosis.* Growth, hyphae, sporangia and spores, exactly as in the species. Oogonia borne racemously on short side branches which are usually very contorted or bent,  $40-80\mu$  diameter, usually  $50-60\mu$ , otherwise as in the species. Oospores 2-10 per oogonium, usually 3-5,  $24-28\mu$  diameter, mostly  $26-27\mu$ , centric. Antheridia clavate, androgynous, arising from main hypha or from oogonial stalk; antheridial stalks often much branched and contorted. Fertilisation tubes seen.

This variety is distinguished from the species by the smaller oogonia, the fewer and larger eggs, and the peculiarly contorted clumps of side branches and stalks. The present observations have shown, however, that forms intermediate in the size of the oogonia and the number and size of the oospores are frequent. For example:

(a) Forms with large oogonia (av.  $70-80\mu$ ) with a few large eggs (av.  $27\mu$ ) were obtained three times.

(b) Forms with smaller oogonia ( $50-60\mu$ ) with smaller eggs (av.  $21\mu$ ) were obtained three times.

(c) Several forms which did not quite correspond in their dimensions to either the species or the variety were also obtained.

It seems, therefore, that these quantitative characters can no longer be used to distinguish the variety. However, the abundant production of side branches and antheridial stalks, themselves much branched and bent, is a distinctive feature which appears to justify the retention of the variety.

3. *Saprolegnia dioica* de Bary in *Bot. Z.* xlvi (1888), 619 (*S. diclina* Humph. in *Trans. Amer. phil. Soc.* xvii (1892), 109; not *S. dioica* Pringsh. or *S. dioica* Schröter).

Figures: Coker, 1923, Pl. 3.

Found six times near Bristol, from October to January.

*Diagnosis.* Growth up to 1.5 cm. long. *Hyphae* up to  $45\mu$  at the base. *Sporangia* and *spores* as typical in the genus. *Oogonia* terminal or intercalary, sometimes up to 5 or 6 in a chain, large, spherical to pear-shaped, or, when intercalary, barrel-shaped; wall pitted rather infrequently;  $45-110\mu$  diameter. *Oospores*, 3-20 per oogonium, usually 8-14, centric,  $20-27\mu$  diameter, av.  $24\mu$ . *Antheridia* diclinous, clavate, several per oogonium; arising on delicate branches which tend to disappear. *Gemmae* numerous, cylindrical, fusiform or pear-shaped; often in chains.

Genus *Achlya* Nees v. Esenbeck, (1823)

(a) *Species already recorded in this country*

4. *Achlya colorata* Pringsh. in *S.B. Akad. Wiss. Berlin* (1882), p. 855 (*Achlya racemosa* var. *stelligera* Cornu in *Ann. Sci. nat. Bot.* xv (1872), 22).  
Figure: Coker, 1923, Pl. 32.  
Found four times near Bristol in November and March.
5. *Achlya polyandra* Hildebrand in *Jb. wiss. Bot.* vi (1867), 258 (*Achlya gracilipes* de Bary in *Bot. Z.* xlvi (1888), 635; not *A. polyandra* de Bary, *Beitr. Morph. u. Phys. d. Pilze*, iv (1881), 49).  
Figures: de Bary *Bot. Z.* xlvi (1888), Pl. 10, 2 and 6.  
Found fourteen times near Bristol from October to March.
6. *Achlya apiculata* de Bary in *Bot. Z.* xlvi (1888), 635.  
Figure: Coker, 1923, Pl. 42.  
Found three times near Bristol in October and January.

(b) *Species new to this country*

7. *Achlya de Baryana* Humphrey in *Trans. Amer. phil. Soc.* xvii (1893), 117 (*Achlya polyandra* de Bary, *Beitr. Morph. u. Phys. d. Pilze*, iv (1881); not *A. polyandra* Hildebrand).  
Figure: de Bary, *Beitr. Morph. u. Phys. d. Pilze*, iv (1881), Pl. 4.  
Found seven times near Bristol from October to December.

*Diagnosis.* Growth up to 1.5 cm. long. *Hyphae* up to  $100\mu$  at the base. *Sporangia* and *spores* typical for the genus: *sporangia*  $350-650 \times 30-60\mu$ ; *spores*  $10-11\mu$  when encysted. *Oogonia* spherical, borne racemosely on short stalks, less than or up to three times the oogonial diameter in length; wall pitted only where the antheridia touch, and not always there; basal wall occasionally protruding into the oogonium;  $45-80\mu$  diameter, usually  $55-60\mu$ . *Oospores* 2-12 per oogonium, mostly 3-6;  $20-24\mu$  diameter, usually  $22-23\mu$ , eccentric. *Antheridia* androgynous or diclinous; stalks branched and sometimes

supplying more than one oogonium; one to several per oogonium. Fertilisation tubes seen. Gemmae cylindrical, formed by segmentation of the hyphae.

7a. *Achlya americana* Humphrey in *Trans. Amer. phil. Soc.* xvii (1893), 116.

Figure: Coker, 1923, Pl. 33.

Found twice near Bristol in December.

*Diagnosis.* Growth, hyphae, sporangia, spores and gemmae as in *A. de Baryana*. Oogonia as in *A. de Baryana* but with conspicuously pitted walls. Oospores as in *A. de Baryana*. Antheridia androgynous, arising from the main hyphae or occasionally from the oogonial stalk.

In addition to the forms referred to *Achlya de Baryana* and *A. americana*, intermediate forms have been found on several occasions:

(a) A form of *A. americana* which had fewer and more inconspicuous pits than usual, and occasional diclinous antheridia.

(b) A form with completely unpitted walls combined with androgynous antheridia.

(c) A form with diclinous antheridia and some pitted walls.

The chief distinctions made between *A. de Baryana* and *A. americana* are that the former has unpitted oogonial walls and some diclinous antheridia, whilst the latter has definitely pitted oogonial walls and the antheridia are consistently androgynous.

Horn (13), however, in an investigation of the effects of changes of nutrition and of temperature on *A. polyandra* de Bary (*A. de Baryana* Humph.), found that many characters formerly considered constant were really very variable. His work goes far to eliminate the distinctions between the two species.

Both Petersen (24) and von Minden (21) reduced the status of *Achlya americana* to *A. de Baryana* forma *americana*, and Coker (2) commented on the impossibility of separating the two species. He found, as has been found in the present work, that forms were constantly obtained which combined the characters of the two, so that these forms could not be certainly referred to one or other of the species. It, therefore, appears that *A. de Baryana* and *A. americana* form a parallel pair to *Saprolegnia ferax* and *S. mixta*. Under constant conditions the two forms normally present distinct characters, but they can be made to vary towards one another in culture, and sometimes do so in natural conditions.

*Achlya de Baryana* is one of the commonest species of the genus in Europe, but up to 1923 (3) it had not been found in America, at least in its typical form. On the other hand, Humphrey (14) stated that *A. americana* was "the most abundant member of the genus and indeed of this family" in the United States, while the only European records of

*A. americana*, up to 1923, were due to Petersen and to von Minden. This seems to indicate that we are dealing with one species which is common on both sides of the Atlantic, and which tends to develop certain characters in the United States, and rather different characters in Europe.

8. *Achlya Klebsiana* Pieters in *Bot. Gaz.* LX (1915), 486.

Figure: Coker, 1923, Pl. 40.

Found six times near Bristol in October and November.

*Diagnosis.* Growth up to 1.0 cm. long. *Hyphae* up to  $85\mu$  at the base. *Sporangia*  $200-700 \times 20-50\mu$ ; secondary sporangia often formed by the outgrowth of part of a hyphal segment cut off below a terminal primary sporangium, sometimes in basipetal succession by repetitions of the process. *Oogonia* in racemes on very short, straight stalks, spherical, sometimes with inward protrusion of the basal wall; pits usually present only where the antheridia touch; diameter  $45-60\mu$ , usually  $50-55\mu$ . *Oospores* 1-13 per oogonium, usually 4-7, eccentric, diameter  $19-25\mu$ . *Antheridia* always didelphous; somewhat elongated and often with foot-like projections touching the oogonia; stalks long, slender and branched. *Gemmae* cylindrical.

This species is very close to *A. de Baryana*. It is distinguished by the very characteristic arrangement of the secondary sporangia, by the slightly smaller oogonia on very short stalks, and by the strictly didelphous antheridia of somewhat different shape.

9. *Achlya caroliniana* Coker in *Bot. Gaz.* L (1910), 381.

Pl. VIII, fig. 1.

Found once near Bristol, in November.

*Diagnosis.* Growth up to 1.5 cm. long. *Hyphae* up to  $70\mu$  at the base. *Sporangia* about  $350 \times 30\mu$ , rarely quite cylindrical. *Spores*  $10.5-12\mu$  in diameter when encysted. *Oogonia* very numerous, small, in a dense raceme on straight stalks which are 1-4 oogonial diameters in length, and sometimes branched at right angles; sometimes spherical, sometimes with one or more papillae; wall unpitted; basal protrusion sometimes present; diameter  $30-40\mu$ . *Oospores* 1-4 per oogonium, usually 1-2, eccentric, diameter  $19-22\mu$ . *Antheridia* may be present on up to 50 per cent. of the oogonia in young cultures, on much branched stalks; androgynous or didelphous; entirely absent from older cultures. *Gemmae* slightly swollen.

Coker<sup>(3)</sup> first stated that antheridia were absent, but later<sup>(4)</sup> he reported that in a form obtained from the soil, antheridia were present on 25-40 per cent. of the oogonia; he did not state the manner of origin of the antheridia, which, in the Bristol material, were as often androgynous as didelphous.

10. *Achlya Orion* Coker & Couch in *J. Elisha Mitchell sci. Soc.* xxxvi (1920), 100.

Figure: Coker, 1923, Pl. 35.

Found four times near Bristol in January and February.

*Diagnosis.* Growth up to 1 cm. long. *Hyphae* up to  $60\mu$  at the base. *Sporangia*  $100-400 \times 20-30\mu$ . *Spores*, diameter  $10\mu$  when encysted. *Oogonia* terminal on main hyphae or in racemes on curved stalks; spherical; walls usually unpitted except where the antheridia touch; diameter  $30-50\mu$ , mostly  $35-40\mu$ . *Oospores* 1-2 per oogonium; eccentric;  $24-40\mu$  diameter, mostly  $27-33\mu$ . *Antheridia* androgynous, clavate, arising from main hyphae or from oogonial stalks; present on most oogonia.

11. *Achlya radiosa* Maurizio in *Mitt. d. dtsh. Fischerei-Vereins*, vii, 1 (1899), 57 (*A. decorata* Petersen in *Ann. Myc.* viii (1910), 522; *A. asterophora* Minden in *Krypt. Fl. d. Mark Brandenburg*, v (1915), 549).

Pl. VIII, fig. 2.

Found four times near Bristol in January and February.

*Diagnosis.* Growth up to 1 cm. long. *Hyphae* up to  $90\mu$  at the base. *Sporangia*  $250-400 \times 25-35\mu$ ; secondary sporangia sparse. *Spores*, diameter  $10-11\mu$  when encysted. *Oogonia* numerous, terminal on main hyphae or in racemes on short stalks; closely set with conical pointed hollow outgrowths; walls unpitted; diameter, without spines  $36-56\mu$ , with spines  $45-75\mu$ ; spines  $8-18\mu$  long and  $7-13\mu$  wide at the base. *Oospores* 1-2 per oogonium, eccentric,  $30-43\mu$  diameter, mostly  $35-38\mu$ . *Antheridia* always present, androgynous, on short curved branches from the oogonial stalks; tuberous, applied near the base of the oogonium by their distal ends; 1-2 per oogonium; fertilisation tubes very frequently seen.

12. *Achlya oblongata* de Bary in *Bot. Z.* xlvi (1888), 646.

Figure: Coker, 1923, Pl. 47.

Found five times near Bristol from September to February.

*Diagnosis.* Growth usually exceeding 1.5 cm. *Hyphae* up to  $130\mu$  at the base. *Sporangia*  $350-600 \times 30-70\mu$ . *Spores*, diameter  $10-11.5\mu$  when encysted. *Oogonia* terminal or on rather long lateral branches, rarely intercalary; oval or pear-shaped; walls unpitted; basal wall occasionally protruding into the oogonium;  $75-150 \times 45-100\mu$ . *Oospores* 2-15 per oogonium, mostly 5-10, subcentric, diameter  $22-31\mu$ , average  $27\mu$ . *Antheridia* dichlorous, one or more per oogonium, on branching stalks; tuberous. *Gemmae* cylindrical or pear-shaped.

12a. *Achlya oblongata* de Bary var. *gigantica* nov.var.

Pl. VIII, fig. 3.

Found twice near Bristol in January.

*Diagnosis.* Growth 2 cm. or more. *Hyphae* up to  $150\mu$  at the base. *Sporangia* as in the species. *Spores*, diameter  $12.5\mu$  when encysted. *Oogonia* in racemes on long lateral branches; oblong, pear-shaped or cylindrical; often with a pointed apex, walls unpitted; very large,  $90-250 \times 50-100\mu$ . *Oospores* 1-8 per oogonium; wall about  $2\mu$  thick;  $36-49\mu$  diameter; frequently not maturing; very dark when young, and structure difficult to observe, subcentric. *Antheridia* diclinous, on most oogonia.

This remarkable variety resembles the species in nearly all respects except in the outstanding size of the oogonia and oospores; the rather cylindrical pointed shape of many oogonia is also characteristic. As compared with the species, a fully grown culture contains fewer mature oospores, of which the structure is rather obscure.

*Achlya oblongata* var. *gigantica* nov.var.

A typo differt oogoniis eximie magnis  $90-250 \times 50-100\mu$ , saepe cylindricis acuminatis; oosporis majoribus  $36-49\mu$  diam. paucioribus (singulis ad octonis).

13. *Achlya megasperma* Humphrey in *Trans. Amer. phil. Soc.* xvii (1893), 118.

Figure: Coker, 1923, Pl. 44.

Found six times near Bristol from January to March.

*Diagnosis.* Growth up to 1.5 cm. long. *Hyphae* up to  $150\mu$  at the base. *Sporangia*  $400-600 \times 40-70\mu$ . *Spores*, diameter  $11.5-13\mu$  when encysted. *Oogonia* in racemes on short, straight stalks; spherical to rather oval; walls unpitted,  $3.5\mu$  thick; protrusion of basal wall frequent. *Oospores* 2-9 per oogonium, usually 3-6;  $43-60\mu$  diameter, mostly  $45-50\mu$ , subcentric. *Antheridia* androgynous or diclinous, on about 50 per cent. of the oogonia; stalks branched and often supplying more than one oogonium. Fertilisation tubes seen. *Gemmae* cylindrical.

The oogonial wall is rather thinner at the point of contact with the antheridium. Numerous much branched side shoots arise from the main hyphae; they resemble antheridial stalks, but usually remain sterile.

14. *Achlya recurva* Cornu in *Ann. Sci. nat. Bot.* xv (1872), 22.

Pl. VIII, fig. 4.

Found eight times near Bristol from October to March.

*Diagnosis.* Growth up to 2 cm. long. *Hyphae* up to  $80\mu$  wide at the base. *Sporangia* about  $355 \times 30\mu$ . *Spores*, diameter  $14-16\mu$  when

encysted. *Oogonia* numerous, in loose racemes on short or long stalks which are usually bent or curved right over; spherical, with many short conical outgrowths; walls unpitted; diameter 45–95  $\mu$ , including spines, usually 70–80  $\mu$ ; spines 7–17  $\mu$  long, 8–11  $\mu$  wide at the base. *Oospores* 1–15 per oogonium, usually 5–8; 25–35  $\mu$  diameter, mostly 27–29  $\mu$ ; subcentric. *Antheridia* androgynous or diclinous; stalks slender and often branched.

15. *Achlya apiculata* de Bary var. *prolifica* Coker & Couch, *The Saprolegniaceae*, 1923, p. 127.

Figure: Coker, 1923, Pl. 43, 2–7.

Found once near Bristol in November.

*Diagnosis.* Growth not exceeding 1 cm. *Hyphae* up to 100  $\mu$  wide at the base. *Sporangia*, *spores* and *gemmae* as in the species. *Oogonia* exceedingly numerous; as in the species but smaller and with more frequent apiculi; 40–75  $\mu$ , usually 50–60  $\mu$ . *Oospores* fewer than in the species, 1–2 per oogonium. *Antheridia* as in the species.

Genus *Dictyuchus* Leitgeb in *Bot. Z.* xxvi (1868), 502.

(a) *Species already recorded in this country*

16. *Dictyuchus monosporus* Leitgeb in *Jb. wiss. Bot.* vii (1869), 357.

Figures: Couch, *Ann. Bot.* XL (1926), Pl. 37 and 38.

Found once near Bristol in September.

On several occasions a growth has been identified as a species of *Dictyuchus* by means of the sporangia, but the oogonia necessary for specific determination could not be obtained even after prolonged cultivation. Since Couch (8) has shown that heterothallism occurs in *Dictyuchus*, it is possible that these non-sexual forms, with similar forms found by other workers, may represent the antheridial or oogonial strains of a heterothallic fungus.

Genus *Calyptalegnia* Coker & Couch in *J. Elisha Mitchell sci. Soc.* XLII (1927), 219.

(b) *Species new to this country*

17. *Calyptalegnia achlyoides* Coker & Couch *loc. cit.* (*Thraustotheca achlyoides* Coker & Couch in *J. Elisha Mitchell sci. Soc.* XXXIX (1923), 112).

Pl. IX, fig. 6.

Found ten times near Bristol from September to March.

*Diagnosis.* Growth up to 2.0 cm. long. *Hyphae* up to 150  $\mu$  wide at the base. *Sporangia* primarily terminal, secondarily cymose, cylindrical, not much wider than the hyphae; 400–900  $\times$  40–70  $\mu$ ; tips blunt;

apex completely removed as a lid at dehiscence. Spores, diameter when encysted  $12-14\mu$ . Oogonia terminal or in racemes, on straight or curved stalks which may be less than, or up to four times the oogonial diameter; spherical; walls unpitted; diameter  $60-120\mu$ . Oospores usually 1-2 per oogonium, rarely 3-4, subcentric,  $55-70\mu$  diameter. Antheridia androgynous, arising frequently from the oogonial stalks; present on most oogonia.

Spore discharge may not occur immediately after dehiscence but the spores may protrude from the opening, giving a characteristic appearance. When the spores are discharged, they escape rather slowly, with an irregular trickling movement. Nearly always, up to half the spores are left inside the sporangium. The discharged spores form a loose mass at the mouth of the sporangium, each encysted as an irregular polyhedron. In a minute or less, reniform zoospores with two lateral cilia emerge from the cysts; the cysts may also germinate by means of a germ tube. Spores left in the sporangium also encyst, and they do not usually develop further, though the cysts may sometimes yield zoospores which leave the sporangium.

Coker and Couch stated that oogonia were rare in their cultures and that attempts to induce their formation by the use of various media were unsuccessful. The material found near Bristol yielded oogonia abundantly.

Genus *Brevilegnia* Coker in *J. Elisha Mitchell sci. Soc.* **XLII** (1927), 207.

(b) *Species new to this country*

18. *Brevilegnia diclina* Harvey in *J. Elisha Mitchell sci. Soc.* **(XLII)**, 1927.  
Pl. IX, fig. 5.

Found once in Bristol in August; in soil from a fern-pot in a hot greenhouse.

*Diagnosis.* Growth up to 1 cm. long. Hyphae up to  $40\mu$  wide at the base, usually up to  $25\mu$ . Sporangia primarily terminal, secondarily cymose, clavate, long or short,  $100-250 \times 10-30\mu$ , sometimes with only a single row of spores. Spores spherical to subspherical, average diameter  $12\mu$ . Oogonia on long, twisted, very narrow and branched stalks (average diameter  $5\mu$ ), which look like a secondary mycelium of small hyphae among the larger hyphae; small, irregular in shape, being rounded with many protuberances;  $18-30\mu$  diameter, mostly  $20-25\mu$ ; walls unpitted. Oospores solitary, eccentric,  $15-22\mu$  diameter, average  $18\mu$ . Antheridia, diclinous, clavate, present on only a few oogonia.

## LEPTOMITACEAE

Genus *Leptomitus* Agardh, 1824

## (a) Species already recorded in this country

19. *Leptomitus lacteus* (Roth.) Agardh, *Syst. Alg.* 1824 (*Conferva lactea* Roth. (*Beitr. z. Bot.* 1789); *Saprolegnia lactea* Pringsh. in *Jb. wiss. Bot.* II (1860), 205; *Apodya lactea* Cornu in *Ann. Sci. nat. Bot.* xv (1872), 5).

Figure: Coker, 1923, Pl. 58.

Found eight times near Bristol from October to February.

Genus *Rhipidium* Cornu in *Bull. Soc. Bot. France*, xviii (1871), 58.

## (b) Species new to this country

20. *Rhipidium europaeum* Minden in *Krypt. Fl. Mark Brandenburg*, v (1912) (*Rhipidium continuum* Cornu and *R. interruptum* Cornu in *Ann. Sci. nat. Bot.* xv (1872), 15).

Text-fig. 1; Pl. X, fig. 8.

Found seven times near Bristol from September to January.

*Diagnosis.* *Thallus* of a large, irregularly cylindrical basal portion, somewhat lobed at the apex and sometimes dichotomously branched. The broad rounded lobes bear very narrow branches, constricted at the point of origin and sometimes along their length; the branches have a bulbous swelling just above the basal constriction. The thallus is attached to the substratum by numerous branched rhizoids, and contains coarse granular protoplasm. Basal portion 400–900 × 30–90  $\mu$ ; wall up to 15  $\mu$  thick; branches 100–500 × 9–14  $\mu$ . *Sporangia* terminal on the branches, with a constriction immediately beneath them; secondary sporangia arise on lateral branches developing from the primaries immediately beneath the sub-sporangial constriction; sympodial groups result from repeated branchings; sporangia oval, with apical dehiscence, 45–70 × 25–47  $\mu$ . *Spores* seen only as rather large rounded masses inside the sporangia. *Oogonia* terminal on narrow branches with sub-oogonial constrictions, spherical to somewhat pear-shaped; walls smooth and unpitted; 47–57  $\mu$  diameter. *Oospores* solitary, walls thick (up to 17  $\mu$ ), sculptured externally, with ridges and points, eccentric, 40–50  $\mu$  diameter. *Antheridia* small 12–16  $\mu$  wide, tuberous, applied to the base of the oogonium; didinious, on much branched stalks.

20a. *Rhipidium europaeum* Minden var. *compactum* nov.var.

Pl. X, fig. 11.

Found three times near Bristol in November and January.

*Diagnosis.* *Thallus* of a very short, broadly cylindrical basal cell

bearing a large number of broad, subdivided lobes, which spread out and around the short stalk in a compact bunch; these lobes bear the narrow branches which are rather shorter than in the normal form. Rhizoidal system relatively well developed, rhizoids stout with rounded tips. *Sporangia* as in the species,  $50-60 \times 25-35 \mu$ . *Oogonia* pear-shaped, smaller than in the species,  $40-45 \mu$  diameter. *Oospores* smaller than in the species,  $28-36 \mu$  diameter. *Antheridia* as in the species.



Text-fig. 1. *Rhipidium europaeum* Minden. Oogonia with antheridia ( $\times 175$ ).

Text-fig. 2. *R. americanum* Thaxter. Narrow branches bearing sporangia and oogonia ( $\times 110$ ).

*Rhipidium europaeum* Minden var. *compactum* nov.var.

A typo differt cellula basali brevissima multilobata; filamentis aliquantum brevioribus; rhizoideis bene evolutis crassis ad apices rotundatis; sporangiis  $50-60 \times 25-35 \mu$ ; oogoniis pyriformibus minoribus  $40-45 \mu$  diam.

21. *Rhipidium americanum* Thaxter in *Bot. Gaz.* xxi (1896), 320.

Text-fig. 2.

Found three times near Bristol in November and January.

*Diagnosis.* Thallus of a large, much branched basal cell, showing successive dichotomy, and attached by numerous rhizoids. The upper

lobes bear many narrow branches constricted at their point of attachment, and constricted beneath the reproductive organs borne upon them. Basal cell, from origin of rhizoids to origin of first lobe,  $500-1000 \times 60-110 \mu$ ; lobes up to  $800 \mu$  long. Narrow branches  $200-800 \times 10-15 \mu$ ; rhizoidal system up to 2 mm. long. Walls up to  $5 \mu$  thick. *Sporangia* terminal, with secondary cymes, ovoid,  $40-110 \times 25-40 \mu$ . *Spores* not seen. *Oogonia* terminal, spherical, smooth-walled,  $40-50 \mu$  diameter. *Oospores* solitary, with thick, ridged wall, eccentric,  $35-45 \mu$ . *Antheridia* androgynous,  $11-14 \mu$  diameter, arising from the antheridial stalks, immediately below the oogonial constriction, rounded, applied to the base of the oogonium. Fertilisation tubes seen.

#### PYTHIOMORPHACEAE

Genus *Pythiomorpha* Petersen in *Ann. Myc.* viii (1910), 494.

(a) *Species already recorded in this country*

22. *Pythiomorpha gonapodiooides* Petersen, *loc. cit.*

Pl. IX, fig. 7.

Found about twelve times near Bristol throughout the year.

Petersen (24) first described this species, but he did not obtain the sexual stage. Von Minden (21) observed oogonia in mixed cultures, and Kanouse (15) obtained the sexual organs in cultures from single spores. My cultures have oogonia, resembling in many respects those described and figured by Kanouse, and, in addition, they yielded oogonia and antheridia of more definite structure; these are regarded as the successfully matured sexual organs.

The oogonia are borne on short lateral branches of the intramatrical mycelium. They are spherical, with a single, thin, unpitted wall. Mature oogonia are dark brown, those with indefinite contents are yellowish brown, and empty oogonia are pale yellow; diameter  $26-35 \mu$ . The oospores are solitary, completely filling the oogonium, with very thick, smooth walls; they are dark brown, centric, and average  $30 \mu$  diameter. Antheridia are clavate; they appear to be present on all oogonia, one to each as a rule; they are  $11-15 \mu$  wide. The apex of the antheridium is attached close to the base of the oogonium. Mature antheridia are dark brown, empty ones are colourless.

The oogonia resembling those described by Kanouse contained evenly distributed protoplasm, completely filling the oogonium, and of indefinite structure. Some had a single thin wall, others contained inside, the thicker wall of the oospore. These oogonia are regarded as immature, or as showing premature arrest of development.

Antheridia occurred on almost all the oogonia in my cultures, whereas Kanouse found them on only about 10 per cent. of the

oogonia. This is not surprising if her material was immature. Kanouse did not comment on the dark brown colour of the sexual organs; this feature is not strongly marked in immature stages.

Mature oogonia show only two walls, the thin oogonial wall and the much thicker wall of the oospore; Kanouse recorded three walls in her material. Her figures, however, give the impression that only two walls were present, since in her drawings the oogonia are surrounded by three lines only. It has not been found possible to confirm the account given by Kanouse of the structure of the wall of the sporangia. She states that the wall becomes differentiated into an outer and an inner layer, separated by a hyaline layer; this has not been seen in the Bristol material, in either mature or empty sporangia.

## BLASTOCLADIALES

### BLASTOCLADIACEAE

#### Genus *Blastocladia* Reinsch. 1878

##### (a) Species already recorded in this country

23. *Blastocladia Pringsheimii* Reinsch. in *Jb. wiss. Bot.* xi (1878), 298.  
Pl. X, fig. 10.

Found six times near Bristol from September to January.

This species has been recorded from a single doubtful specimen obtained by Barnes and Melville(1); therefore, although the present finds do not constitute a new British record, it seems suitable to give a full diagnosis.

*Diagnosis.* Thallus consisting of a stout basal cell, either simple or much lobed apically; the lobes may be branched, their apices becoming swollen and bearing the reproductive organs. Numerous branching rhizoids attach the base of the thallus to the substratum. The wall is thick and scaly, and the lobes are reticulately marked by scars of old sporangia. Protoplasm rather dark, containing many spherical oily globules. Simple or branched sterile hairs, with bulbous bases, arise from the basal cell or from its lobes. The whole plant, including the rhizoids, may be up to 2 mm. long; the basal cell is  $400-1000 \times 50-200 \mu$ ; the lobes are  $240-400 \times 80-160 \mu$ ; the wall is up to  $8 \mu$  thick; the sterile hairs are  $2-5 \mu$  diameter. Sporangia sessile on the swollen apices of the lobes, cylindrical, fusiform to nearly ovoid, thin-walled, with a basal septum; dehiscence apical, with exit papilla when ripe; the empty sporangia fall away;  $150-250 \times 30-47 \mu$ . Spores seen only in sporangia, or rounded off owing to interruption of spore discharge; diameter  $11-14 \mu$ ; apparently they do not emerge in a vesicle. Oogonia sessile, oval or rounded, with a thin wall; average diameter  $50 \mu$ . Oospore solitary, completely filling the oogonium, with

a very thick, regularly pitted wall; contents very oily; the oospore escapes from the oogonium before germination.

### SUMMARY

An examination has been made of the natural waters of the Bristol district, using methods recommended by American workers. Twenty-two species of aquatic fungi have been found, fourteen of which have not before been recorded in this country; these have been fully described.

#### *Species found*

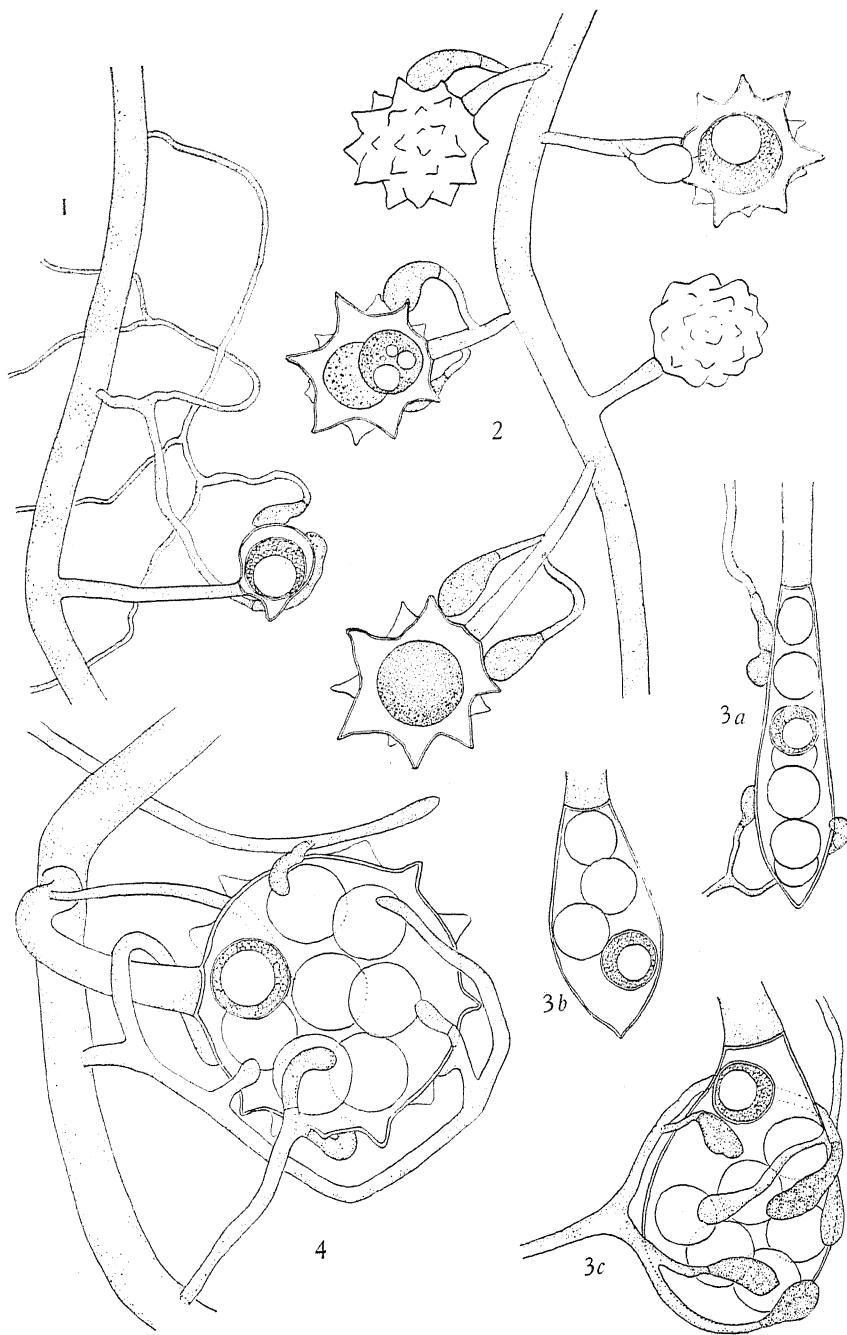
(a) Species already recorded in this country: *Saprolegnia ferax* Kützing, *Achlya colorata* Pringsheim, *A. polyandra* Hildebrand, *A. apiculata* de Bary, *Dictyuchus monosporus* Leitgeb, *Leptomitus lacteus* Agardh, *Pythiomorpha gonapodiooides* Petersen and *Blastocladia Pringsheimii* Reinsch.

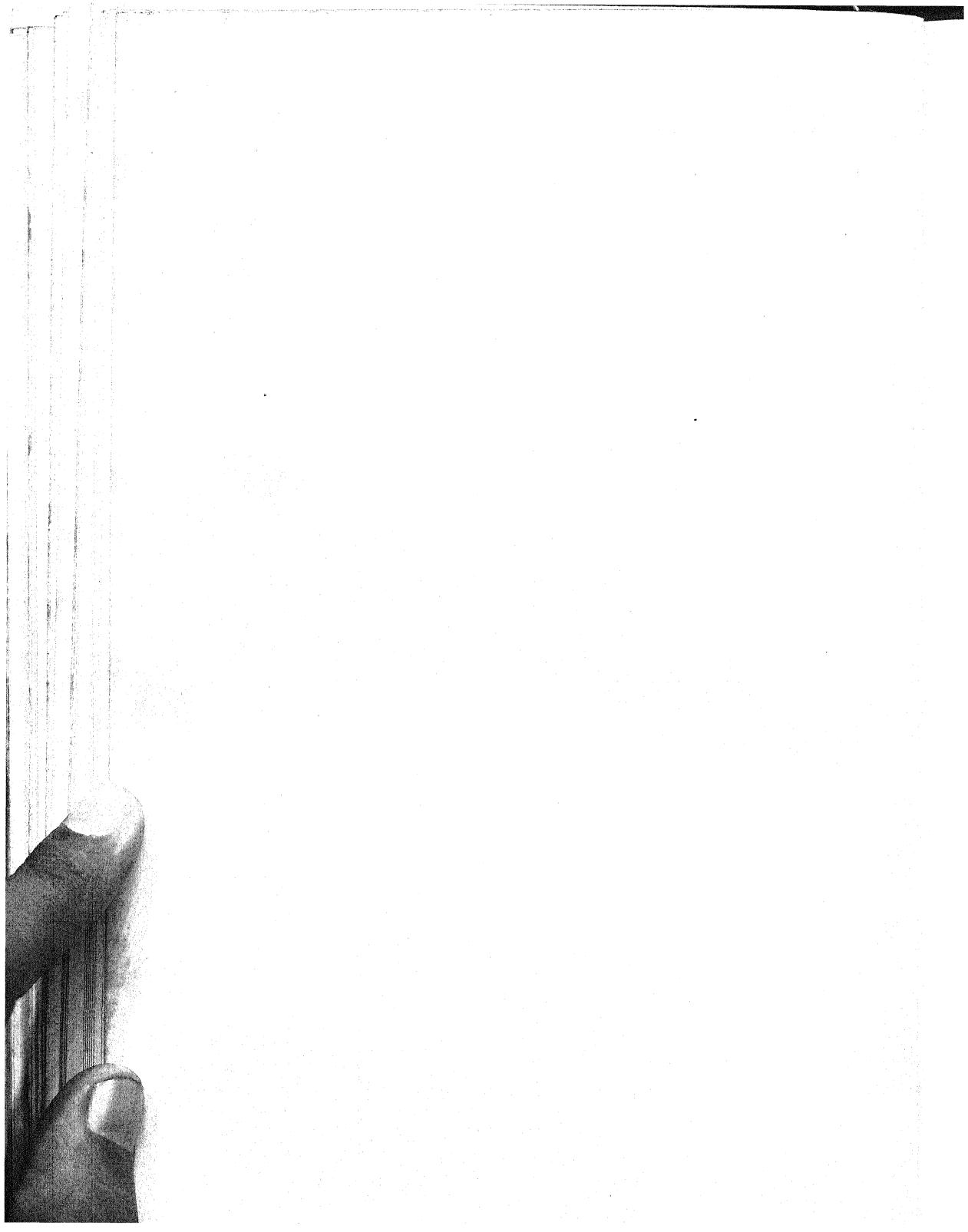
(b) Species new to this country: *Achlya de Baryana* Humphrey, *A. Klebsiana* Pieters, *A. caroliniana* Coker, *A. Orion* Coker & Couch, *A. radiosa* Maurizio, *A. oblongata* de Bary, *A. oblongata* var. *gigantica* nov.var., *A. megasperma* Humphrey, *A. recurva* Cornu, *A. apiculata* var. *prolifica* Coker & Couch, *Calyptalegnia achlyoides* Coker & Couch, *Brevilegnia diclina* Coker, *Rhipidium europaeum* von Minden, *R. europaeum* var. *compactum* nov.var., *R. americanum* Thaxter.

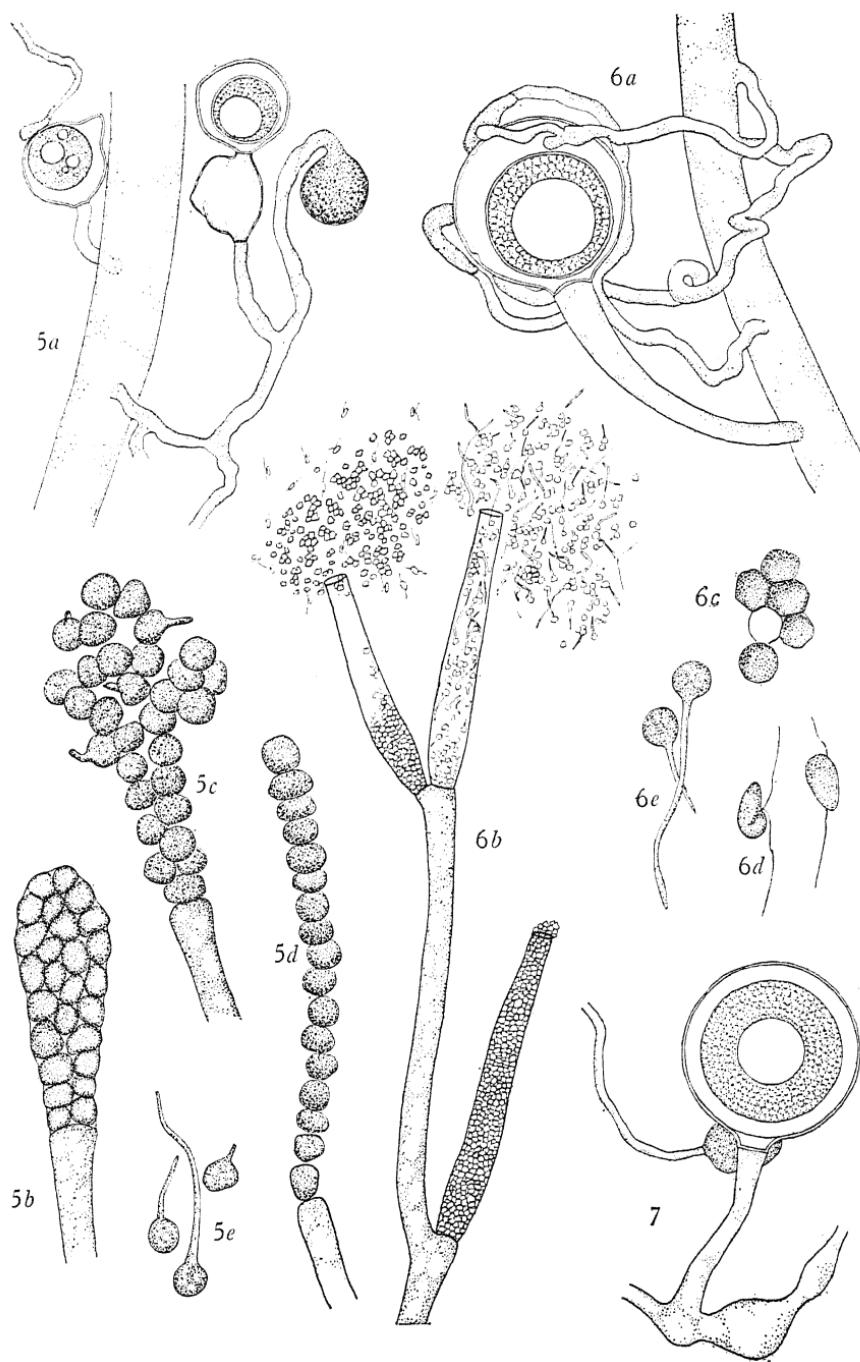
I am indebted to Prof. O. V. Darbshire and to Prof. W. H. Lang, F.R.S., for facilities extended to me during the preparation of this paper. I also wish to thank Dr Ivimey Cook for his helpful and unfailingly kind supervision of the work presented here.

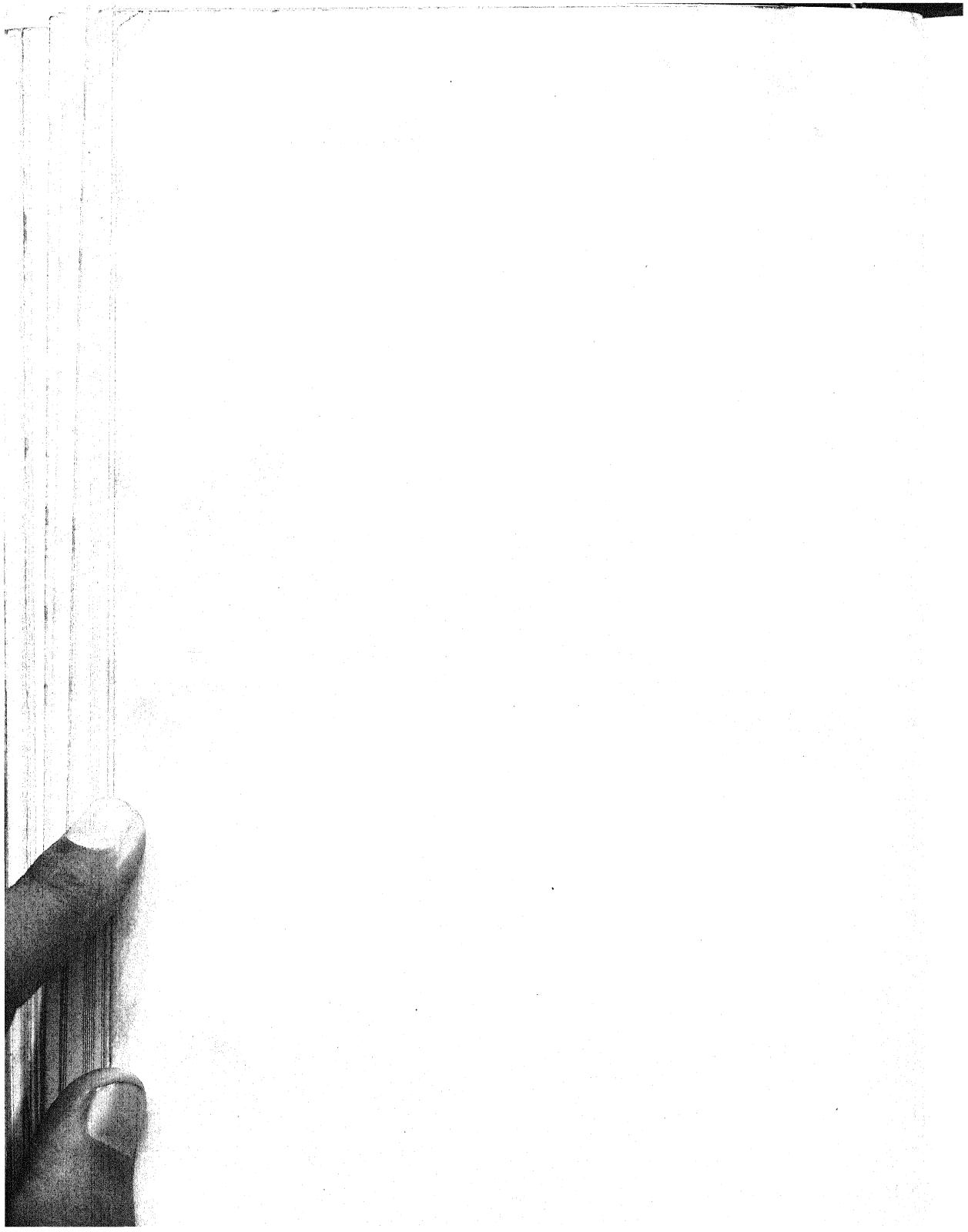
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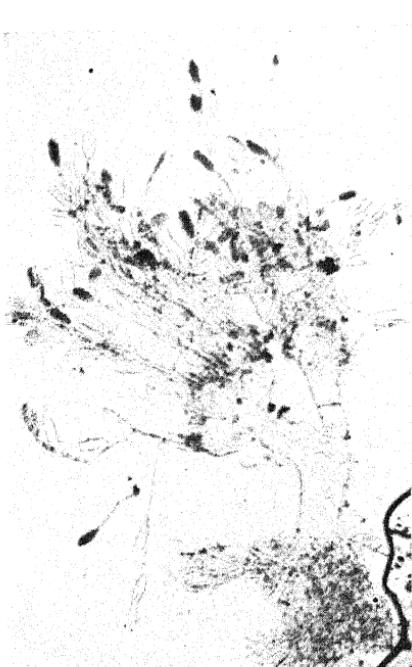
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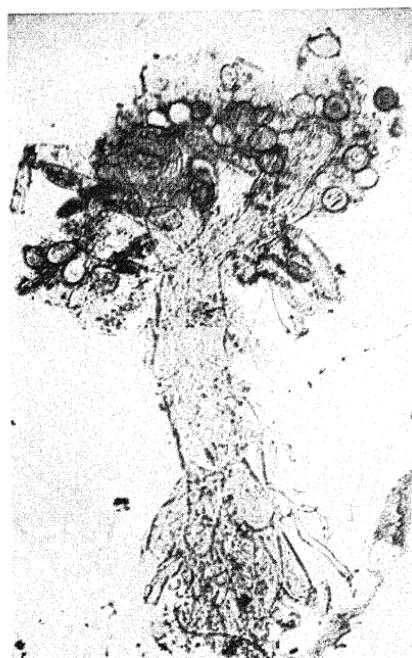




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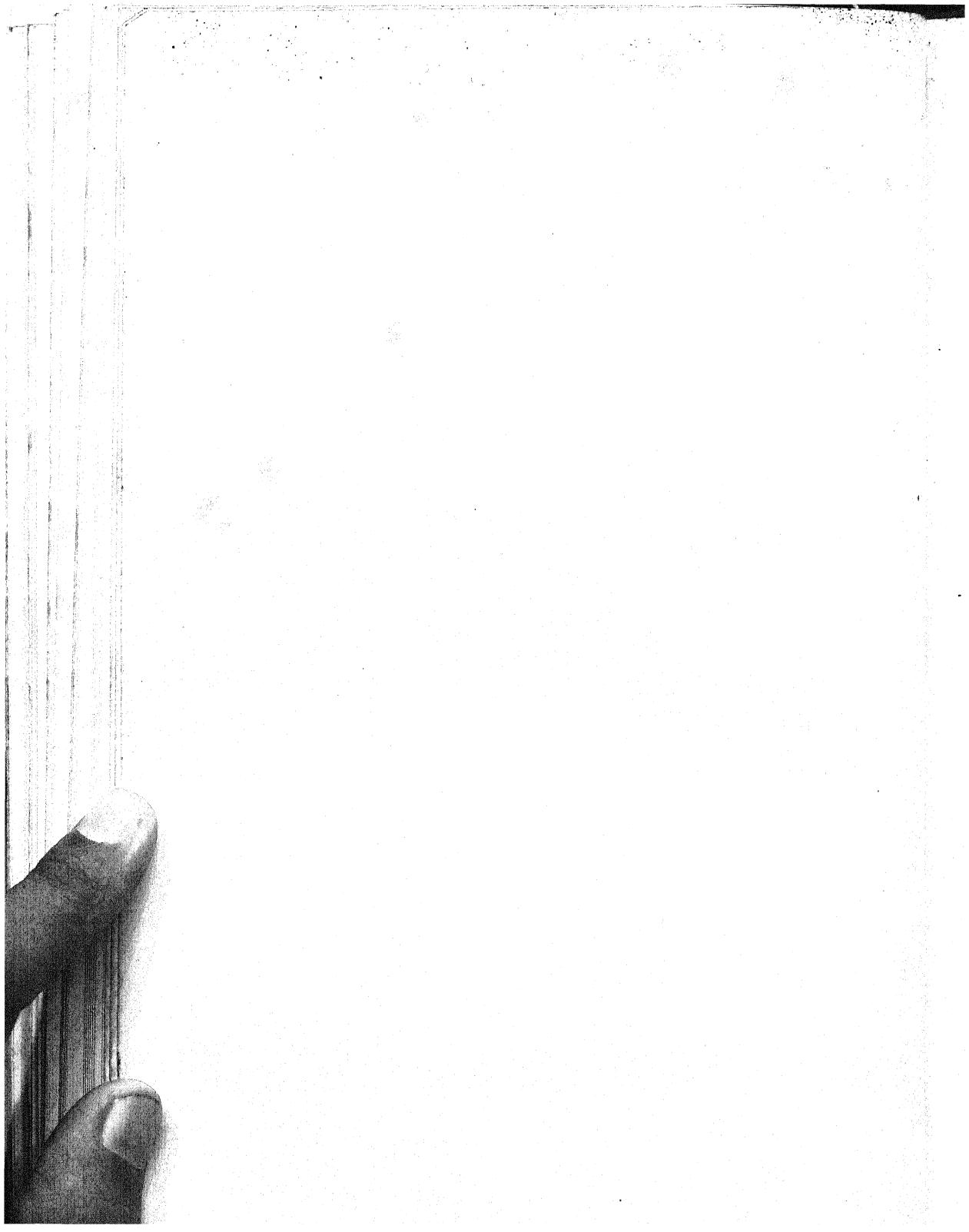
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#### EXPLANATION OF PLATES VIII-X

##### PLATE VIII

Fig. 1. *Achlya caroliniana* Coker. Oogonium with androgynous antheridia ( $\times 175$ ).  
 Fig. 2. *A. radiosa* Maurizio. Hypha with oogonia and antheridia of various ages ( $\times 125$ ).  
 Fig. 3. *A. oblongata* var. *gigantica* nov.var. (a), (b) and (c). Oogonia and antheridia ( $\times 82$ ).  
 Fig. 4. *A. recurva* Cornu. Oogonium with antheridia ( $\times 175$ ).

##### PLATE IX

Fig. 5. *Brevilegnia dictina* Harvey. (a) Oogonia of various ages ( $\times 285$ ). (b) Ripe sporangium. (c) Spores freed by disappearance of sporangium wall. (d) As in (c), with spores in linear arrangement. (e) Germinating spores. (b), (c), (d) and (e)  $\times 175$ .  
 Fig. 6. *Calyptalegnia achlyoides* Coker & Couch. (a) Oogonia with antheridia ( $\times 110$ ). (b) Sporangia, showing types of spore-behaviour ( $\times 50$ ). (c) Encysted spores, with one emerging from its cyst. (d) Swimming spores. (e) Spores germinating by hyphae. (c), (d) and (e)  $\times 375$ .  
 Fig. 7. *Pythiomorpha gonapodiooides* Petersen. Oogonium with antheridium ( $\times 750$ ).

##### PLATE X

Fig. 8. *Rhipidium europaeum* von Minden. Mature thallus showing sporangial stage ( $\times 70$ ).  
 Fig. 9. *R. americanum* Thaxter. Young thallus with developing sporangia ( $\times 50$ ).  
 Fig. 10. *Blastocladia Pringsheimii* Reinsch. Mature thallus with sporangia and oogonia ( $\times 50$ ).  
 Fig. 11. *R. europaeum* var. *compactum* var.nov. Young thallus with sporangia ( $\times 70$ ).  
 N.B. Except in (11), the rhizoidal systems are for the most part missing.

## AN EXPERIMENTAL AND CYTOLOGICAL STUDY OF THE LIFE HISTORY OF ENDOPHYLLUM SEMPERVIVI

By DOROTHY ASHWORTH

(Research Scholar, University College, Nottingham)

(With 23 Text-figures)

THE genus *Endophyllum* was one which aroused interest at an early period in the investigation of the plant rusts, by reason of its special short-cycled nature, for only the two spore forms, spermogonia and aecidia, occur. A further interest was added when it was found that, although the spores which developed in association with the spermogonia were borne in sori that had morphologically the appearance of aecidia and were therefore termed aecidiospores, they behaved like teleutospores in giving rise to a promycelium and sporidia.

The first study of *Endophyllum Sempervivi* was undertaken by de Bary (6). He stressed the apparent anomaly of an aecidium producing spores, the subsequent germination of which showed them to be the equivalent of teleutospores. He figured the germination of one of these, the infection of the host tissue by the basidiospores, and he reported the presence of a perennial mycelium. He also described certain plants of *Sempervivum* infected with *Endophyllum* on which he had never seen the development of spermogonia, although the aecidia were produced with normally developed and fertile spores. It is unfortunate, in view of more recent work on this fungus, that the nuclear content of these spores was not known. The continued seasonal occurrence of such a form is easily explained by the peren-nating mycelium.

Later Maire (10) described the cytological phenomena accompanying the germination of the aecidio-teleutospores, as they had come to be named. He reported that these were binucleate and that the two nuclei passed into the germ tube without fusion, and there divided to give a four-segmented promycelium.

It was not until 1914 that Hoffmann (8) published his more comprehensive study of the complete life history of the fungus. He reported the initiation of the diplophase by equal cell fusion at the base of the aecidial primordium as in other rusts, although the point at which the fusion occurred was not so well marked as in certain of the

forms previously investigated, nor was the evidence produced so convincing. The binucleate cells thus formed cut off binucleate cells which divided to give rise to intercalary cells and aecidiospores. Thus far, the behaviour of the spore-producing primordium was that of a typical aecidium, but it was established that, instead of these binucleate spores continuing the diplophase, fusion of the conjugate nuclei took place as soon as the spore was detached from the chain. A reduction division might follow this fusion immediately or during the germination of the spore, and as this was followed at once by a second division, the mature spore might appear quadrinucleate. The four nuclei so formed were later separated by wall formation in the promycelium and each passed out to a basidiospore.

Moreau (17) substantiated this work, but also discovered a different course of events for a strain of *Endophyllum Semperfervivi* (13) which he found on *Sempervivum* in a cemetery near Bagneaux. Here the two nuclei in the young aecidiospores did not fuse but underwent conjugate division, and the spore thus became quadrinucleate. Subsequently two of these nuclei degenerated, and later the two remaining might fuse. No mention was made of spermogonia in this form.

There is thus considerable conflict of evidence centred round the nuclear events in the aecidiospore, and this is only intensified by comparison with events in what appear to be nearly related forms.

*Endophyllum Euphorbiae-sylvaticae* on *Euphorbia amygdaloides* was investigated by Sappin-Trouffy (20) and described in his comprehensive review of the Uredinales. He found no fusion in the aecidiospore, nor did he consider that there was evidence for a reduction division, as both the nuclei passed into the promycelium and divided conjugately, although the four nuclei so formed became separated in the promycelium by their cross walls. "Par conséquent il n'y a pas de raison pour identifier cette germination avec celle d'une téleutospore comme on l'a fait jusqu'à ce jour." The value of these observations is enhanced by the fact that in all other rust genera he had studied, Sappin-Trouffy found a nuclear fusion in the teleutospore which to him indicated fertilisation; in *Endophyllum* his results were therefore contrary to expectation.

Later, Moreau (14, 17) described a strain of *Endophyllum Euphorbiae-sylvaticae* which was uninucleate throughout its development. The single nucleus in the aecidiospore divided to give a four-nucleate mycelium. No spermogonia were reported.

Poirault (18, 19) found a uninucleate form of *Endophyllum Centranthi-rubi*. There were no cell fusions in the aecidial primordium. Here, however, the nucleus underwent only a single division and the promycelium was consequently only two-celled and abstricted two sporidia.

Maire (10) found a further variation in *Endophyllum tuberosae*. The

aecidiospores were at first binucleate, but became uninucleate by degeneration of one of the nuclei. The persistent nucleus passed into the promycelium, and was cut off from the body of the spore by a septum. A nuclear division followed and resulted in a two-celled promycelium, but since the nucleus of the lower compartment degenerated, a single sporidium only was abstracted from the tip of the promycelium.

Thus in what is at present regarded as a single genus, there is considerable variation in the development, and it may be necessary to conclude with Moreau: "Pour nous, le nom d'*Endophyllum* n'est pas un nom générique, il ne désigne pas un groupe naturel constituant une unité systématique, il désigne un type de développement caractérisé par la germination des écidiospores en promycelium."

The present study of *Endophyllum Sempervivi* was started primarily to investigate the function of the spermatia, but since such cytological variations had been reported for this species it was considered desirable to work out the developmental history of the particular strain of the fungus under investigation.

#### MATERIAL AND METHODS

Material of *Endophyllum Sempervivi* was first obtained in February 1932 through the kindness of Mr J. Ramsbottom. It was growing on plants of *Sempervivum tectorum* and *S. Webberi*. At this time a considerable infection was apparent; the spermogonia appeared as innumerable minute red specks, whilst the aecidia showed as white spherical pustules of considerable size below the epidermis of the leaves. During the second and third seasons observations were again made on these plants, on a further supply sent by Mr Ramsbottom and also on those plants which had been inoculated with sporidia in the summers of 1932 and 1933. Generally speaking, the infection of these latter plants was lighter than in the others. *Sempervivum tectorum* was used exclusively as the host plants in the infection experiments. In the first season healthy plants of this species were obtained from the Royal Holloway College Botanical Garden where the work was being done, and in the second season Dr B. Barnes very kindly provided a most liberal quantity.

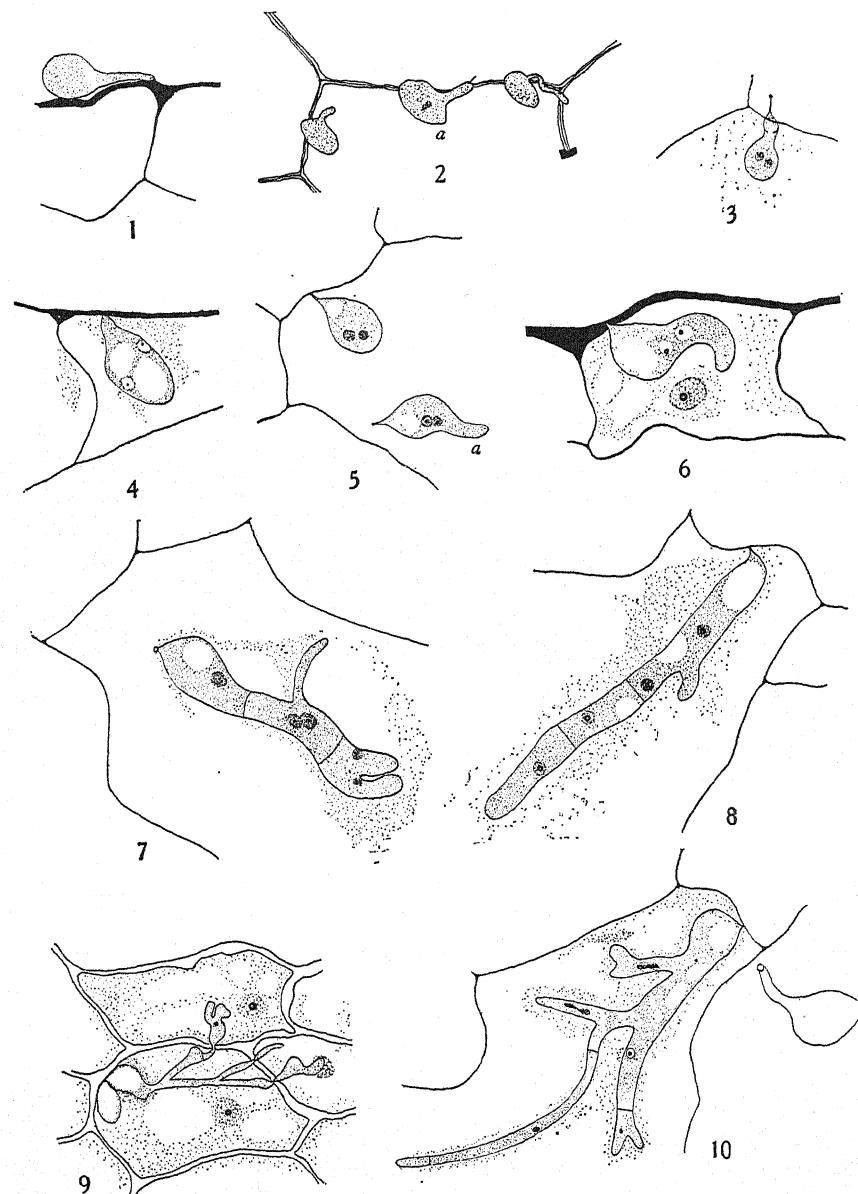
As in the other rusts studied, mono-sporidial and multi-sporidial infections were made. As the mycelium is perennial it was early realised that only a single sporidium per plant could be used in inoculation, to test the homothallic nature of the fungus. The methods for making these inoculations were exactly described in an earlier paper for *Puccinia Malvacearum* (4). A slight difference was made in the preparation of the inoculum. The aecidiospores were germinated in moist chambers on agar films and the sporidia were picked up directly from these films.

For cytological investigations, material was fixed in Allen's Bouin, Flemming's weaker solution and 2B.D.(4) as used at the John Innes Horticultural Institute. Sections were cut at thicknesses from  $4\mu$ - $8\mu$  and stained in iron alum haemotoxylin or Gram's iodine gentian violet, with Congo red, erythrosin, or light green in clove oil as a counter stain. All methods gave similar results.

#### THE LIFE CYCLE

The aecidiospores of *Endophyllum Semperfivi* are formed at the beginning of the growing season of the host plant, and germinate as soon as the aecidia are open, to give a promycelium which abstracts sporidia. Out of doors this usually takes place towards the beginning of April and the spores remain viable until the early days of June. In the summer of 1932 spores were germinated successfully from April 15th until June 12th. On plants grown in a slightly heated greenhouse, however, in 1933 and 1934, the aecidia matured much earlier and germination of the spores was obtained as early as March 1st, but no material was germinable after the first week of May.

The sporidia are at first uninucleate, but they become binucleate by a precocious nuclear division even whilst attached to the sterigma. If they fall on the surface of the host plant under the most favourable conditions of temperature and moisture, they will send out a germ tube (Fig. 1). This is usually formed by elongation of the hilum of the spore, and during the process vacuolation of the spore protoplasm occurs although the nuclei remain in the body of the sporidium (Fig. 2a). From the tip of this germ tube a penetration-hypha is put out which pierces the cuticle and wall of the epidermis of the host. This minute penetration-hypha often traverses the wall for a considerable distance and through it the contents of the spore pass (Fig. 3). During transit the nuclei must undergo distortion. The precocious nuclear division to give two nuclei of less bulk is possibly correlated with the necessity of passing through so small an aperture. It may be, too, that if one nucleus becomes damaged the second one can carry on development. Once through to the cell lumen, the tip of the penetration-hypha expands forming a minute spherical swelling in which the two nuclei can be seen (Fig. 3). As this vesicle increases in size vacuolation occurs and a little later the part remote from the point of entry becomes differentiated as a thinner type of hypha (Figs. 5a, 6). The primary infection-hypha reaches this stage of development within twenty-four hours. During the second day it becomes septate. The end nearer the point of entry retains its expanded form and becomes more and more vacuolate as the hypha grows in size (Fig. 7). Although the binucleate nature of the sporidium has often been reported in other rusts the problem as to how the binucleate hypha becomes uninucleate has not been satisfactorily solved. Deposits of tannin in the



Text-figures 1-10

epidermal cells of the *Sempervivum* leaf render observation difficult, but in this species of *Endophyllum* it seems that either one nucleus only divides and that between these two nuclei a septum is formed so that the cell nearer the point of entry is binucleate and the other uninucleate (Fig. 8) or *vice versa* (Fig. 7). As a matter of fact there is considerable variation in the distribution of nuclei and in the septation of this primary infection-hypha. When it is three or four cells in length each of the cells puts out a lateral branch of rather less diameter than that of the parent cell (Fig. 7). These lateral branches grow rapidly and soon penetrate the wall and invade the surrounding tissues (Fig. 9). Those which enter neighbouring epidermal cells frequently end in a haustorium (Fig. 9), but the mycelium thus formed is composed of uninucleate cells.

Instead of forming spermogonia and aecidia immediately, the intracellular mycelium becomes partly intercellular and passes through the leaf towards the base, and there enters the cortex of the underground stem. This occurs fairly rapidly. For example, a plant inoculated on April 15th showed hyphae in all parts of the leaves infected, including the base by May 5th. The leaves were then removed, to determine whether the fungus had yet entered the stem. In the spring of 1934 this plant showed no infection, so that it was evident that the fungus had not passed into the stem.

Subsequently the mycelium perennates in the underground stem but does not approach the extreme tip. In consequence of this, the new leaves formed at the centre of the rosette between May and the end of the growing season are free from disease. At the end of the year the mycelium passes upwards to the growing point of the host. If a longitudinal section is cut through this region towards the end of November or the beginning of December, a considerable quantity of mycelium can be distinguished, which is characterised by its irregular form and numerous and stout haustoria (Fig. 11). It does not approach the meristematic region of the tip nor does it invade the vascular tissue.

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LEGENDS TO TEXT-FIGURES 1-10

Fig. 1. Transverse section of epidermal cell of *Sempervivum tectorum* with a germinating sporidium.  $\times 2000$ .

Fig. 2. Sporidia on the surface of the host cells. The centre one shows a short germ tube and the fine penetration-hypha.  $\times 1400$ .

Fig. 3. The spherical vesicle in the host cell. Note the point of entry and the fine penetration-hypha.  $\times 2000$ .

Figs. 4, 5, 6. Similar binucleate stages; in Fig. 6 the elongation of the infection-hypha has started.  $\times 2000$ .

Fig. 7. A three-celled stage. The centre cell is putting out a lateral branch.  $\times 2000$ .

Fig. 8. Another three-celled stage.  $\times 2000$ .

Fig. 9. Young infection invading adjacent cells. Note the haustoria.  $\times 1400$ .

Fig. 10. Similar infection. The empty sporidium can be seen on the right.  $\times 2000$ .

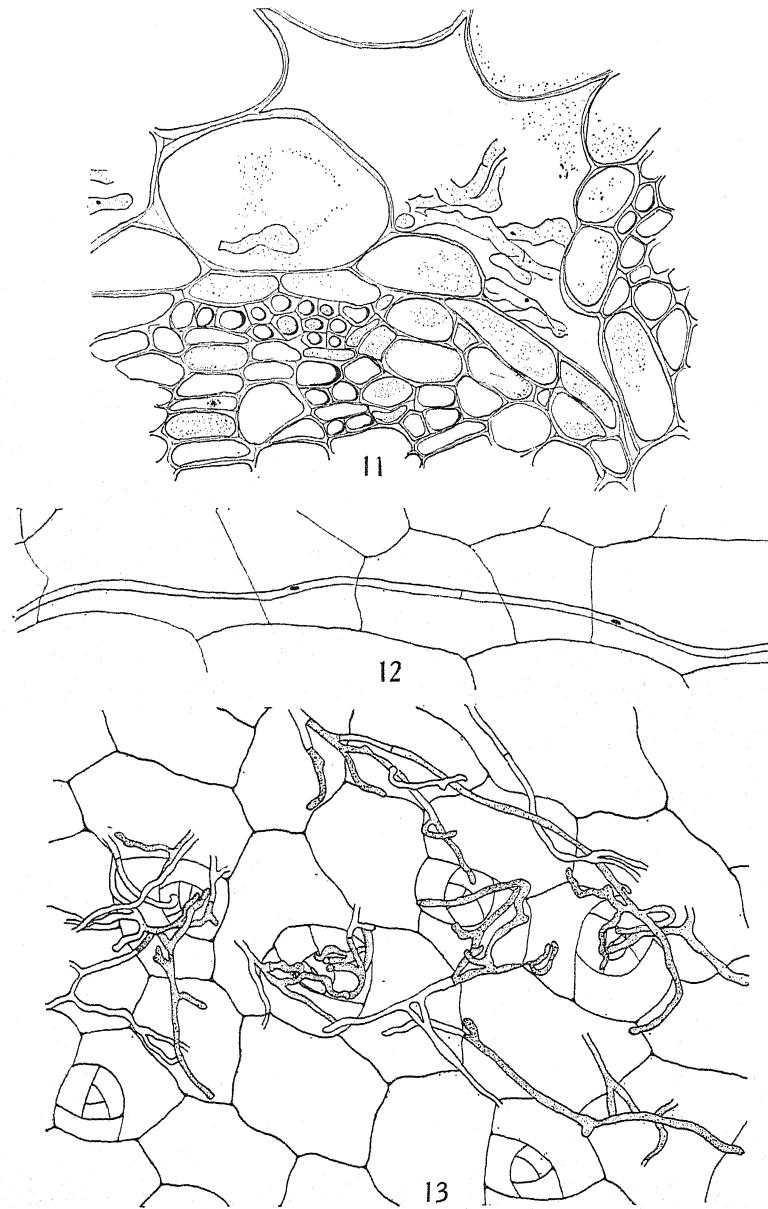


Fig. 11. Perennating mycelium in the cortex of the host. Underground stem.  $\times 1400$ .

Fig. 12. Hypha in leaf at the beginning of the year. Note the unbranched mycelium.  $\times 1400$ .

Fig. 13. Mycelium in the subepidermal region of the leaf. The mycelium is grouped beneath stomata.  $\times 760$ .

The renewal of activity of the mycelium in the spring coincides with the growing season of the host. An early spring or higher artificial temperature will cause the *Sempervivum* plants to sprout early. The first outward signs of the disease are the slightly yellower colour and abnormal elongation of the leaves. The mycelium in the leaves is thinner than that of the underground stem and possesses fewer haustoria. It is characterised by a marked growth in the direction of the longer axis of the leaf (Fig. 12), and the cells, though greatly elongated, are uninucleate. No hyphal fusions were observed in the material examined.

The accompanying figures from the leaves of a healthy and a diseased plant respectively are of interest as showing the effect of the fungus on the leaf at this stage. Figs. 14a and 14b show that there is a marked difference between the form of the epidermal cells. In the healthy leaf (Fig. 14a) the walls appear corrugated, whilst in the diseased leaf (Fig. 14b) these corrugations have almost disappeared owing to the elongation of the cells in a sagittal direction. In transverse sections (Fig. 15a, b) the cells of the healthy plant appear slightly larger than those of the diseased one, but in longitudinal sections (Fig. 16a, 16b) there is a most striking difference in size shown, which accounts for the considerable elongation of the diseased leaf. Hypertrophy is caused by changes in size and shape of the individual cells rather than in an increase in number.

Subsequently the hyphae become localised in the subepidermal layer of the leaf. There is a considerable massing of hyphae in the substomatal spaces (Fig. 13). There seem to be three possibilities for the further development of these knots of hyphae; they may function as primordia of spermogonia, they may function as primordia of aecidia, or they may remain as substomatal hyphae.

The hyphae which protrude through stomata are in every respect similar to the receptive hyphae described by Andrus (3) for *Uromyces appendiculatus* and Allen (1, 2) for *Puccinia triticina* and *P. coronata*. They were of very frequent occurrence in the earliest stages of the disease. A connection could sometimes be traced between these hyphae and other branches of the mycelium connected to haustoria. This suggests that the hyphae are not trichogynes, since a trichogyne would be attached to a reproductive structure and not to a vegetative organ such as a haustorium.

When a hyphal knot is destined to form a spermogonium the mycelium branches repeatedly at close intervals and the branches become arranged approximately parallel to one another, though owing to their tapering form they converge to a common centre (Fig. 17). The occurrence of spermogonia below stomata is most marked. There appears to be no sheathing peridium, but the circle of hyphae at the extreme edge become differentiated as paraphyses. At

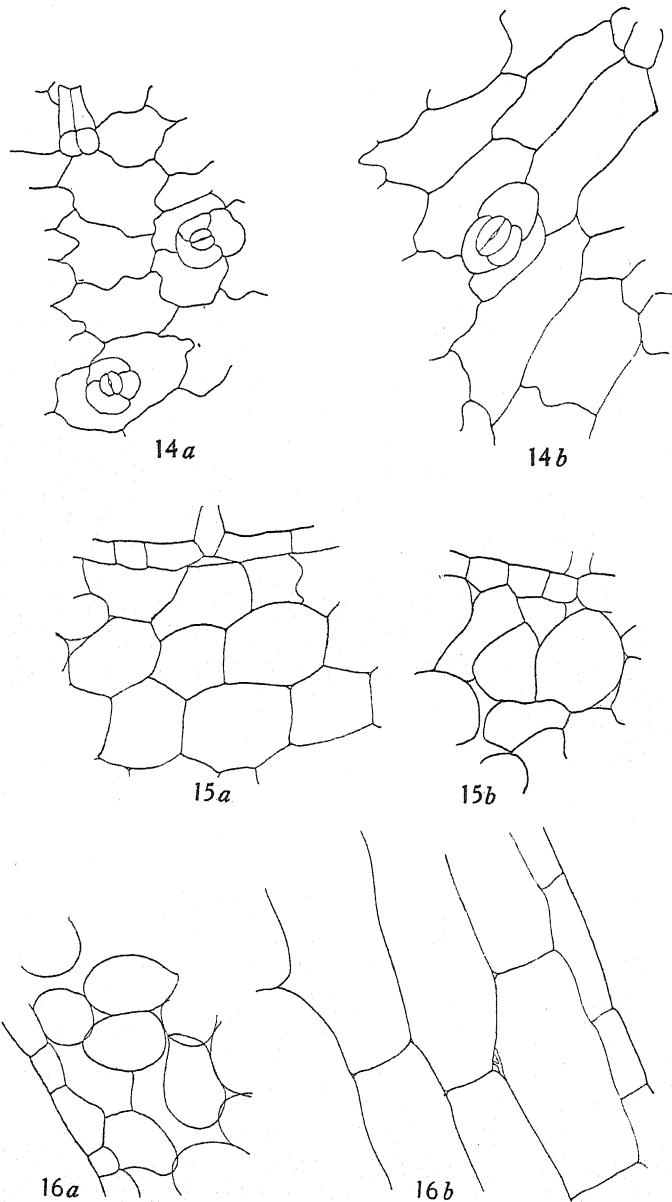


Fig. 14a, b. Epidermal strips of a healthy and a diseased leaf of *Sempervivum Webberi*.  
Fig. 15a, b. Transverse sections of healthy and diseased leaves.  
Fig. 16a, b. Longitudinal sections of a healthy and a diseased leaf respectively.

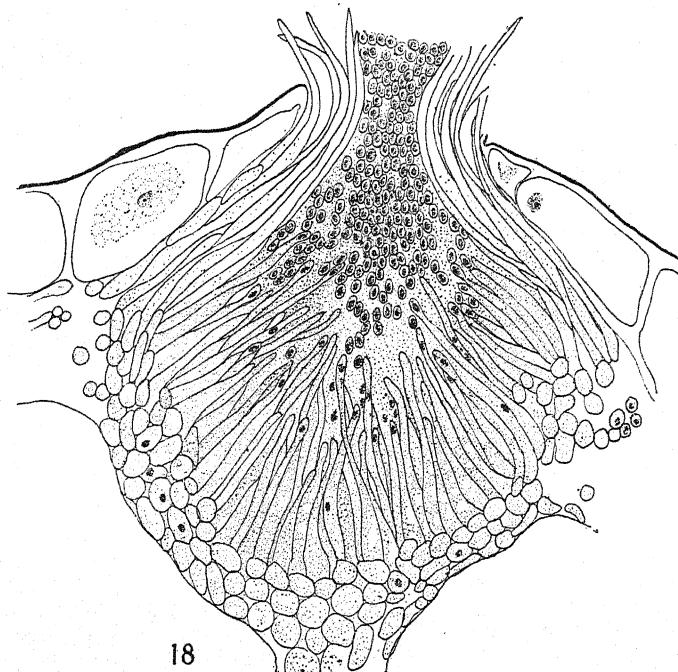
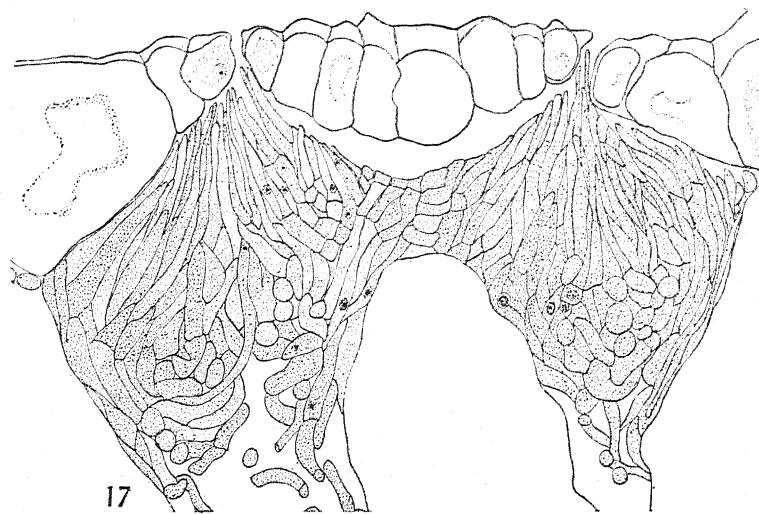


Fig. 17. Two young spermogonia. Note their relation to the stomata.  $\times 760$ .

Fig. 18. Mature spermogonium with sheathing paraphyses and many spermatia.  $\times 760$ .

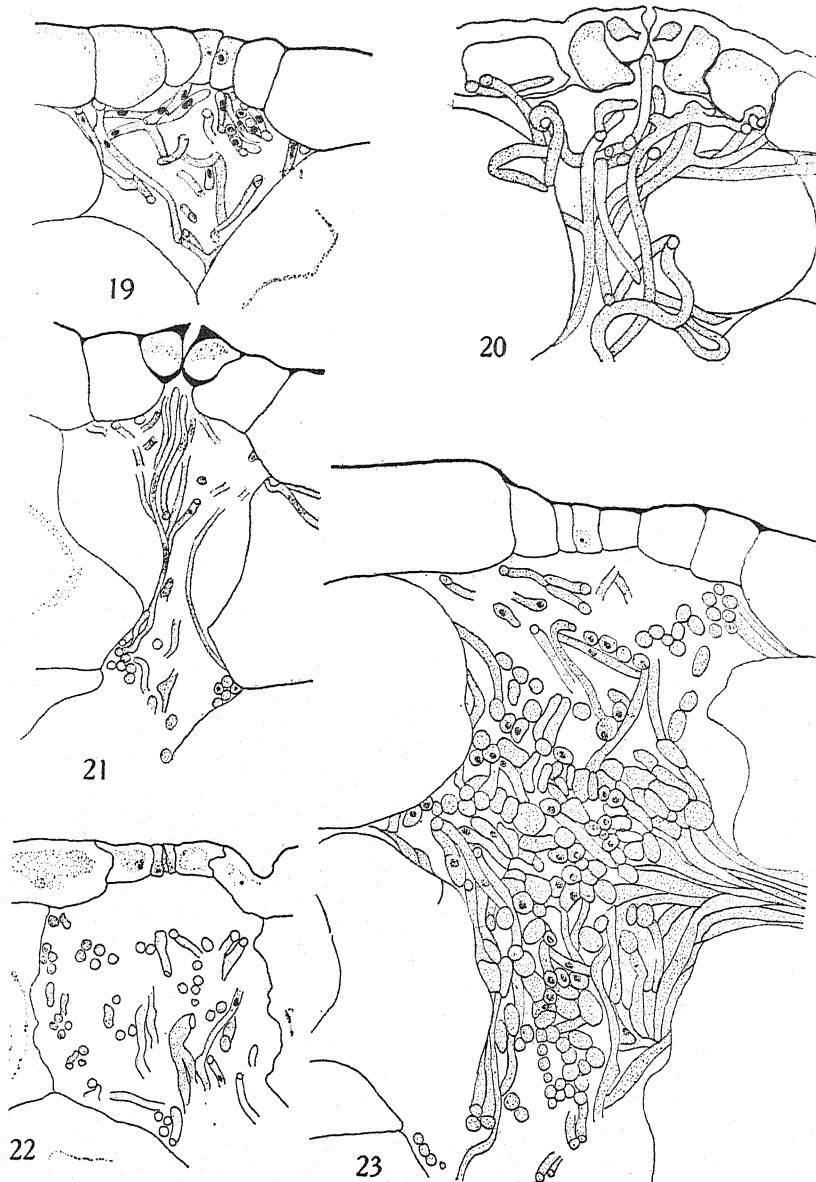
first the spermogonia appear as minute yellow dots beneath the epidermis, but later they assume a bright red shade owing to the colour of the paraphyses, which protrude through the ostiole, and when aged become dark brown and then black. The spermatia are abstracted from the spermatiophores in the usual way by budding, and are rather blunt with the large nucleus which is so characteristic of the spermatium (Fig. 18). There seemed to the naked eye to be little spermogonial nectar but sections of fixed material through ripe spermogonia show masses of spermatia adhering together in spherical drops. A mature spermogonium is about  $200\mu$  in diameter.

In 1933 the first spermogonia were found as minute specks on February 7th and by February 15th these were abstracting spermatia.

Aecidial primordia usually accompanied these, forming small whitish flecks beneath the epidermis. These were composed of less tightly packed wefts of uninucleate mycelium. The hyphae were stouter than those of the spermogonia or the perennating mycelium (Fig. 23). Towards the end of February the primordia had increased greatly in size, and a differentiation could be seen between the three or four layers of cells adjacent to the leaf tissues and the inner weft of mycelium. Cytological examination showed all these hyphae to be uninucleate, and those of the inner region more vacuolate.

Later in the month, certain cells at the base of the aecidium appeared richer in protoplasmic content than the rest and more active. It was difficult to determine whether these hyphae were of new growth or whether they were due to the differentiating tissues, but in view of their subsequent history, the first alternative seems more probable. The component cells were uninucleate.

At this stage the white colour of the primordia was replaced by a rusty tinge. It is interesting to recall that a similar change of colour marked the change from the uninucleate to the binucleate condition in *Puccinia Malvacearum* and has been noted also in *P. Poarum*. Binucleate cells were found mingled with the uninucleate ones, in the tightly packed mass of tissue at the base of the aecidium. Hoffmann (8) figured nuclear migration and remarked that the points at which it took place were less definitely marked than in other rusts. In the present investigation a few possible nuclear migrations have been seen. Once the cells become binucleate, they divide rapidly, the nuclei undergoing conjugate division. Each of these cells is an aecidiospore initial and divides further to give an aecidiospore and an intercalary cell. Quadrinucleate cells may be seen occasionally in the chains. These appear to be cells in which wall formation had not been completed after conjugate division. Meanwhile the more loosely woven tissue which had previously filled the aecidium breaks away to make room for the advancing column of cells enclosed in the peridium. Subsequently the aecidiospores become rounded off by



Figs. 19, 20. Young spermogonia. Fig. 20 was drawn from living material.  $\times 760$ .

Fig. 21. Hyphae making their way to a stoma.  $\times 760$ .

Fig. 22. Young aecidium. Note the wider more loosely woven hyphae.  $\times 760$ .

Fig. 23. Slightly older aecidial wort, still uninucleate.  $\times 760$ .

thick walls. Amongst these are seen quadrinucleate cells, which may be regarded as spores in which precocious meiosis had taken place. Their thickened walls seemed to differentiate them from those described above. Uninucleate aecidiospores in which fusion of the conjugate nuclei had occurred were not of frequent occurrence, and from this it would seem that there is a very short resting stage before the fusion nucleus undergoes meiosis.

There are two further points of interest to note: firstly, the large number of non-viable spores which frequently appeared white externally, and secondly, the association of the aecidia with stomata. Sometimes as many as three stomata were seen in one section.

The pressure of the ripe aecidiospores causes the peridium to split. There is no definite ostiole in this rust. Frequently the aecidia are visited by small insects, which can sometimes be seen feeding on the spores.

Carefully fixed material of germinating aecidiospores reveals that meiosis occurs in the promycelium, and all stages of these divisions have been obtained. It is suggested that the four-nucleate cells noted above, in which it was thought meiosis might have occurred, are non-viable, because no germ tubes have been seen which enclosed more than a single nucleus in the young stages.

#### EXPERIMENTAL WORK

Craigie's (7) work on *Puccinia Helianthi*, *P. graminis* and other rusts suggests that the spermatia of these fungi are functional, although how they function has not yet been satisfactorily demonstrated. The evidence is well known and is, briefly, that pustules of mono-sporidial origin form only spermogonia, unless spermatia of a complementary nature are added to them. The importance of the study of the development of the rust fungi in single-spore culture has thus been revealed. The presence of a perennating mycelium in this rust (*Endophyllum Sempervivi*) renders it necessary that these mono-sporidial inoculations should be confined to a single sporidium per plant, and theoretically in such cultures one would expect to get only spermogonia the following spring. If more than one sporidium were introduced, there is a possibility of the inter-mixing of the mycelia in the root stock. A certain number of such inoculations were attempted, but were considerably limited in number by greenhouse accommodation, and it was felt that another method of tackling the problem might give better results.

The aim of the experimental work was to determine whether aecidia of a normal type developed if the intervention of the spermatia were eliminated. The plants of *Sempervivum tectorum* were favourable objects for such treatment, as the volume of the leaf occupied by the fungus was small compared with the leaf itself, and so

the spermogonia could be treated without causing too much injury to the leaf tissue. Consequently, as soon as the first signs of elongation were seen in the infected plants at the beginning of the year, these were watched carefully for the appearance of spermogonia. As soon as these were seen as tiny specks beneath the epidermis of the leaf they were removed.

In the first group of experiments this was effected by burning them out with a red-hot needle. Care was taken to heat the needle well between each prick, so that there was no possibility of any "mixing" effect, and the spermogonia were treated before they broke through the epidermis. As controls in this experiment, an undiseased plant of *Sempervivum* was treated in the same way to see the effect of the hot stabs on the tissue of the leaf, and a diseased plant was left untreated. The plants were examined each day and developing spermogonia were removed.

Three plants were treated in this way:—in plant A all the spermogonia were removed, in plant B those on the upper surface only and in plant C those on the under surface. The following tables summarise these results. In Table I the daily development of spermogonia is recorded for plant A in which all the spermogonia were removed. In Table II the weekly counts of spermogonia and aecidia are given for plants A, B, C and the Control.

These tables show the following points clearly: (1) in all plants spermogonia developed quite rapidly in spite of treatment, and (2) the greater development of spermogonia and aecidia always took place at the lower surface. The first signs of aecidial primordia were seen on February 10th, and they gradually enlarged. By February 19th the colour of the aecidia had changed to yellow and by February 21st the first ones were open.

This experiment is open to two main criticisms. In the first place it may be argued that the normal physiological processes of the leaf have been interfered with and consequently changes introduced which are not conducive to the further development of the fungus. In those plants in which the spermogonia were removed from the one surface only, no difference in the time of appearance or ripening of the aecidia was detected. The second criticism is that since these plants were in a greenhouse with other infections, spermatia might have been carried by insects and other agencies to the plants from which the spermogonia had been removed and so assured the development of aecidia, not through the spermogonia since they had been removed, but by means of the "receptive" hyphae. Another plant was therefore treated in the same way: all the spermogonia were removed, but the plant was isolated from any possible infection in the laboratory, and aecidia were formed.

The second method was that of treating the leaf surfaces with a

Table I. *The daily development of spermogonia and aecidia in Plant A*

Date	Number of spermogonia	Number of aecidia
February		
7	37	—
8	59	—
9	90	—
10	135	—
11	165	—
12	105	—
13	81	32
14	51	—
15	5	—
16	16	—
17	13	—
18	—	—
19	27	—
20	30	42
21	57	—
22	49	—
23	9	—
24	35	—
25	—	—
26	—	—
27	1	69
28	—	—
March		
1	—	—
2	—	—
3	—	—
4	—	—
5	—	—
6	—	79

Table II. *Weekly counts of spermogonia and aecidia on upper and lower surfaces of five leaves*

Date ...	Feb. 13th		Feb. 20th		Feb. 27th		Mar. 6th		Total
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	
Plant A									
Spermogonia	88	178	91	197	122	230	124	232	356
Aecidia	16	5	18	10	21	16	25	23	46
Plant B									
Spermogonia removed on the upper surface only									
Spermogonia	145	238	128	265	130	278	130	278	408
Aecidia	45	121	50	111	52	119	53	126	179
Plant C									
Spermogonia removed on the lower surface only									
Spermogonia	—	—	86	195	88	215	88	215	303
Aecidia	—	—	23	40	27	43	27	43	70
Control									
(For four leaves)									
Spermogonia	95	146	165	174	197	198	197	198	395
Aecidia	11	6+ $\rho^*$	34	43	44	38	38	45	83

\*  $\rho$  = primordia of aecidia which appear as whitish specks.

smear so that the spermatia set free from the spermogonia were held in place and could not mix. Two kinds of smear were used, (a) one which would keep the spermatia in place and (b) one which would kill them as well as prevent them from being dispersed. Vaseline and liquid paraffin were used for the first type. As in the above experiment, three plants were used. In one both leaf surfaces were smeared, in a second the upper surface only and in a third the lower surface only. In the plants treated with vaseline, only one application was made, for it was realised that repeated application might cause mixing of the spermatia and yet not be definitely toxic to them.

In the plants in which both surfaces were smeared no complete development of the fungus was obtained. This seems due to the disturbance of the normal physiological processes of the leaf rather than to the elimination of the work of the spermatia, for the plants became unhealthy. In those in which one surface only was treated, spermogonia and aecidia were formed profusely in the plants treated with vaseline. The liquid paraffin seemed to have a more injurious effect than the vaseline, as it ran down the leaves and collected at the crown of the plant.

The two toxic smears used were (a) a fine suspension of shellac in alcohol used for fixing pencil and charcoal drawings and supplied by Rowney's under the trade name "Fixatif" and (b) a smear containing a 0.01 per cent. mercuric chloride solution in such quantities of liquid and solid paraffin as to give a fluid of suitable consistency. Its adherence to the leaf surface was ensured by the addition of glycerine. In the experiment with "Fixatif" this was sprayed on the plant daily; the aecidial primordia were seen on February 20th and they developed normally. In the plants treated with mercuric chloride daily the one in which both sides of the leaf were treated died. The other two plants in which the upper and lower surfaces were treated, respectively, formed aecidia on both surfaces. It is interesting to note that Stevens (21) found a  $N/6400$  or 0.002 per cent. solution of mercuric chloride sufficiently toxic to prevent the germination of *Uromyces* spores, so that it seems safe to assume in this experiment that development of the aecidia was completed without the intervention of spermogonia.

It remained to determine if the aecidia formed in all these experiments were of the normal type, and if the spores were viable and germinated normally. Comparative examination of carefully fixed material of the control plants and those experimentally treated revealed no difference in development, all the spores arising from binucleate basal cells. The spores subsequently became uninucleate and always germinated to give a four-celled promycelium, abstricting four sporidia.

From these experiments one definite conclusion can be reached.

Aecidia can complete their development without the intervention of spermatia. The initiation of the binucleate stage may be effected by hyphal fusions. Whether this is the usual method still remains to be proved, by evidence showing that ripe aecidia are not developed in mono-sporidial culture. In a rust like *Endophyllum Sempervivi*, with a perennating mycelium, the possibilities of such fusions appear to be greater than in one in which the infection is only local. During the present investigation, however, no binucleate cells have been seen prior to the development of the aecidia.

#### SUMMARY

1. The sporidia of *Endophyllum Sempervivi* are precociously binucleate.
2. Entrance to the host cell is gained by penetration of the epidermal wall by a fine hypha.
3. The infection vesicle is at first a spherical binucleate sac.
4. Elongation of the part most remote from the point of entry occurs, and subsequent septation takes place.
5. Further growth results in the production of a mycelium of uninucleate cells which is inter- and intra-cellular and passes down to the base of the leaf where it enters the stem.
6. No hypertrophy of the leaves occurs at this stage.
7. Perennating mycelium spreads through all the tissues of the stem except the vascular tissue and the apical meristem, and there passes the winter.
8. On renewal of activity in the spring, the mycelium passes to the leaves and causes hypertrophy by elongation.
9. It becomes massed in the subepidermal tissues, especially in the substomatal spaces.
10. Emergent hyphae are frequently seen protruding through the stomata.
11. Spermogonia are the first organs to be developed and occur markedly below stomata.
12. These are accompanied by wefts of aecidial primordia composed of uninucleate cells.
13. Later a secondary growth appears at the base and the hyphae become binucleate.
14. The diplophase may be initiated by nuclear migration.
15. The nuclei of each binucleate cell divide conjugately and from the aecidiospore mother cell formed an aecidiospore and intercalary cell are produced.

16. The spores may be quadrinucleate whilst still enclosed in the peridium.

17. They germinate to give rise to a three-septate promycelium and abstract four sporidia.

18. Experiments made to determine the function of the spermatia show that the mature aecidia can be formed when the spermatia are (a) removed by burning out with a hot needle, or (b) kept in position by the application of a smear, e.g. vaseline, liquid paraffin, "Fixatif" or a solution of mercuric chloride.

In conclusion I should like to express my thanks to Miss E. M. Blackwell and Prof. H. S. Holden for their help and criticism at various stages of the work.

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## SOME FURTHER NOTES ON THE PRESERVATION OF PETRI DISH CULTURES

By S. P. WILTSHERE  
(*Imperial Mycological Institute, Kew*)

FOUR years ago I described a method of preserving Petri dish cultures of fungi (*Trans. Brit. mycol. Soc.* xv (1930), 93-5), but since then experience has revealed some difficulties that had not before been encountered. The manner in which these may be overcome, together with some slight improvements in the technique, are now recorded as a supplement to the previous paper.

Firstly, very old cultures have been found not to adhere well to the wax. The reason for this is not clear. The agar, which is thickest at the edge as it runs up the side of the glass, is more or less rounded at the bottom rim as moulded by the Petri dish, and besides this, in old cultures the surface of the agar is usually covered with a thick growth of mycelium which hinders drying; these factors may prevent the agar when permeated with hyphae from taking a good grip on the wax. Or possibly the real cause may lie in a physical change in the agar itself, perhaps simply the partial drying up which occurs in old cultures. But whatever the reason may be, there is a tendency for the agar to curl away from the wax in drying, and to prevent this, two methods have been adopted. The first is to cut off the edge of the cultures at an angle of 45°, the top of the cut being innermost; this should leave the lower margin closely applied to the wax and the operation should be carried out by drawing a scalpel round the culture after it has been transferred to the disk for drying. The thin margin of the agar dries rapidly and gives the culture a good hold. The second method is to examine the drying culture five or six hours after its transfer to the disk and, if any peeling off has occurred, to press the extreme edge of the agar gently but firmly down. In this way it is usually possible to make it adhere again to the wax. These methods apply particularly to old cultures, as cultures not more than fourteen days old usually dry quite satisfactorily without either trimming or pressing and should, therefore, be used whenever possible.

The second difficulty was occasioned by the slowness of the drying due to coldness and dampness of the atmosphere. In such circumstances, it was found advisable to use some form of heat, and this practice, which has since proved advantageous for regular routine, is

recommended where any difficulty in drying is experienced. The heat derived from two 10-watt electric light bulbs connected in series has been found quite sufficient, drying the cultures within twenty-four hours, frequently less. This gives a temperature of approximately 23° C. to an inverted culture placed about 7 cm. directly above the lamp. The only danger is that the wax may become too soft in hot weather; a slightly plastic wax enables the drying culture to take a firm grip of it, but too soft a wax allows the drying agar to draw it up into wrinkles. Temperature conditions can be regulated by raising or lowering the drying culture and little difficulty has been found in making the adjustment. With care, hot-water radiators can be utilised as a source of heat.

Thirdly, instead of transferring the cultures by hand from the Petri dish to the drying disk it is sometimes a good alternative to float them out in water in a photographic dish. When the edge of the agar culture has been loosened, the Petri dish is held vertically and slowly lowered a little way into the water, the edge of the agar being raised by a lifter and induced to float on the surface. The Petri dish is gradually lowered more deeply into the water, at the same time very slowly rotated, preferably counter-clockwise, and gradually inclined to the horizontal, while the agar is separated from the glass by the lifter. Great care must be taken to prevent the water from flowing over the surface of the culture, which is somewhat difficult when the aerial mycelium is only poorly developed. By this procedure it is possible to loosen a culture which may have adhered to the glass by appressoria, and however fragile the agar may be, it can usually be transferred without being broken. Finally, the Petri dish is completely submerged and the agar culture floats free on the surface of the water. It can be gently guided over the drying disk already placed in the water in the photographic dish and the disk raised, leaving the agar culture lying flat on its surface. By adopting this method any kind of medium may be used for the culture; potato dextrose agar and Dox, as well as clear maize agar have consistently given satisfactory results.

Lastly, the black film of the ferrototype plate is liable to become detached round the cut edge in course of prolonged use and a stove-enamelled disk, with sloping edges and enamelled after being cut, has proved more efficient. The wax solution previously recommended must always be used in cleansing it. The disk may be mounted in the centre of a wooden tray\* into which the wax can be melted. The use of such a tray has been found convenient, as the wax can be renewed without difficulty and the surface readily remade by flaming with a Bunsen.

\* The drying disk with tray can be obtained from Messrs. Baird and Tatlock (London), Ltd., 14-17 Cross Street, Hatton Garden, London, E.C. 1.

## STUDIES ON BRITISH PYRENOMYCETES

I. THE LIFE HISTORIES OF THREE SPECIES  
OF *CEPHALOTHECA* FUCK.

By CHAS. G. C. CHESTERS

(With Plates XI and XII and 5 Text-figures)

## I. INTRODUCTION

It is proposed to publish the results of a series of investigations by pure culture methods of the life histories of selected species of Pyrenomycetes, paying particular attention to the development of the imperfect stages and to the development and cultural requirements of the ascophorous stages where these are obtained. Pyrenomycetes are known mainly in their perfect stage, and precise information of the imperfect condition is often lacking. Generic and specific diagnoses which may later be used in an attempt to indicate the evolution of the group as a whole should be on a wide comparative basis. The immediate necessity appears to be to provide detailed accounts of the development of the spore-bearing structures of definite species.

Winter (10), following Fuckel, retained the genus *Cephalotheca* in his suborder Perisporiae of the Pyrenomycetes, but Fischer (3) placed it in the Aspergillaceae which he treated as a family of his new order, Plectascineae, definitely removed from the Pyrenomycetes. Von Höhnel (5) suggested that the genus should be transferred to a separate family, Cephalothecaceae, which, though related to Aspergillaceae, contained types with a specialised perithecial structure for the liberation of the ascospores. In this he was followed by Nannfeldt (7). It is not intended to consider here the validity of Pyrenomycetes as a specialised class within the Ascomycetes; in this series of papers the word is used in the sense employed by Winter.

In order that the systematic position adopted may be clear, a summary is given below, and the reasons which led to this will be discussed in later sections.

*Cephalotheca* Fuck. *Symb. Myc. Nachtr.* 1 (1871), 9 (297).

Syn. *Crepinula* O. Kuntze, *Rev. Gén. Pl.* II (1891), 850.

*Fairmania* Sacc. in *Ann. Mycol.*, IV (1906), 276.

*Aposphaeriopsis* Died. *pro parte* in *Ann. Mycol.* XI (1913), 44.

*Fragosphaeria* Shear in *Mycologia*, XV (1923), 124.

- (1) *C. sulfurea* Fuck. Type species, *loc. cit.*
- (2) *C. reniformis* Sacc. & Therry apud Sacc. in *Mich.* II (1881), 312.  
Syn. *Fairmania singularis* Sacc. *loc. cit.*  
*Aposphaeriopsis fusco-atra* Died. *loc. cit.*
- (3) *C. purpurea* (Shear) comb.nov.  
Syn. *Fragosphaeria purpurea* Shear, *loc. cit.*

## II. COMPARISON OF MATERIAL COLLECTED WITH AUTHENTIC MATERIAL AND ORIGINAL DESCRIPTIONS

Each field collection of the species investigated from which monosporic cultures were obtained was compared either with authentic material or, failing this, with the original diagnosis. All the material which I have examined or which has been examined on my behalf is given below.

- (1) *C. sulfurea* Fuck.

*Authentic material.* Fuckel, *Fungi Rhenani*, 2313, preserved in the Herbaria of: (1) The British Museum, general fungus collection. (2) C. E. Broome; incorporated in the British Collection in the British Museum. (3) The Pathological Collection, Bureau of Plant Industry, Washington, U.S.A.\* (4) The Royal Botanic Garden, Kew.† (5) The Botanischer Garten und Museum, Berlin Dahlem (specimen kindly loaned by Prof. Dr E. Ulbrich).†

*British Material.* C. E. Broome's material was collected at: (a) Bristol, April 1876, and (b) Henbury, October 1879.

*Material used for isolation.* Collected by W. B. Grove, on garden cane, Birmingham, 1931. Preserved in my herbarium, No. 4.

- (2) *C. reniformis* Sacc. & Therry.

No authentic or other material available for comparison. (The type specimen is cited by G. Gola (1930) in *L'erbario Micologico di P. A. Saccardo*, p. 165, as being preserved in Saccardo's herbarium.)

Material used for isolation was collected on dead beech, Richmond Park, Surrey, September 1931 (No. 1167) and June 1932 (No. 1223) by Mr E. W. Mason, and on dead oak, Birmingham, June 1933 (No. 5) and February 1934 (No. 67) by myself.

- (3) *C. purpurea* (Shear) comb.nov.

*Authentic material.* In Herbarium C. L. Shear: pure culture tube No. 4821, on corn-meal agar (cf. Shear *loc. cit.* p. 125).‡

Material used for isolation was collected by Mr E. W. Mason on

\* C. L. Shear, *in litt.*

† Without any discernible fungus, E. W. Mason, *in litt.*

‡ I am indebted to Dr Shear not only for comparing with his type specimen isolations from collected material sent to him, but also for providing me with a slide from his specimen.

dead beech, Richmond Park, Surrey, July 1932 (No. 1228), and on dead oak, April 1933 (No. 12 of my herbarium).

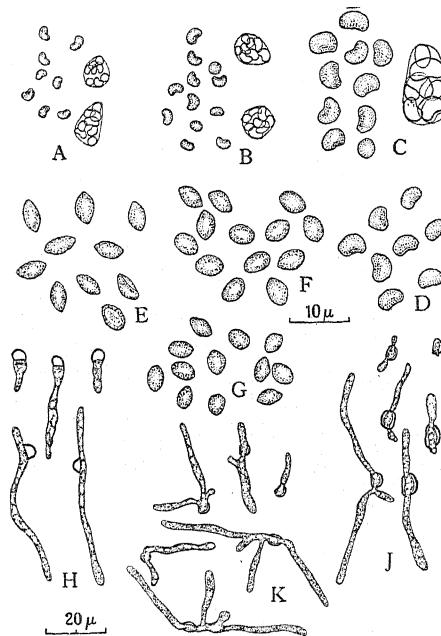
(1) *C. sulfurea* Fuck.

The genus was founded on *C. sulfurea* and *C. trabea*. The former was placed first, has been recognised since on more than one occasion, and is universally recognised as the type species.

The collection made by W. B. Grove consists of discrete groups of astomous perithecia of various ages surrounded by a sulphur-coloured villus of rather flexuose hyphae (Pl. XI, fig. 1). The young perithecia are totally embedded in the general mycelium and are individually covered by sulphureous hyphae (Pl. XI, fig. 1 A). The mature perithecia (250–500 $\mu$  in diameter) are glabrous at the apex, black, and have a series of definite suture lines regularly disposed over their surface (Pl. XI, fig. 1 B). The polygonal areas delimited by these sutures are often torn apart, revealing a mass of brown ascospores (Pl. XI, fig. 1 C). The oldest perithecia are completely shattered and only a basal cup remains in which the ascospores are loosely held together in small clusters (Pl. XI, fig. 1 D). The perithecia, though embedded in mycelium, are not immersed in the substance of the cane. The ascospores, which are elliptical to ovate (Text-fig. 1 E) and individually of a light brown, measure 4.5–6  $\times$  3–4 $\mu$  (mostly 6  $\times$  4 $\mu$ ). Ascii attached to ascogenous hyphae were not observed in this material, but Fuckel (*loc. cit.*) describes the ascii as forming globose clusters at the ends of branched hyphae. Von Höhnel<sup>(5)</sup> stated that the perithecia of this species, in addition to being fragile, break up along definite suture lines such as those which have been described above.

The two specimens of *Fungi Rhenani*, No. 2313, in the Herbarium of the British Museum, bear numerous groups of young and adult perithecia enclosed within a definitely sulphureous villus. The mature, but unshattered, perithecia are from 330 to 500 $\mu$  in diameter, and in both specimens perithecia having sutures can be observed. The ascospores are elliptical or ovoid (Text-fig. 1 F) and measure 4–6  $\times$  3–4 $\mu$ . The characteristic size appears to be 6  $\times$  4 $\mu$ , and no ascospores longer than 6 $\mu$  have been observed. Hence Fuckel's original measurement of 6–7  $\times$  3 $\mu$  is in need of some slight emendation. The specimen in the Pathological Collection of the Bureau of Plant Industry, Washington, was examined by Dr C. L. Shear who states (*in litt.*) that: "The perithecia are covered with a sulphur-colored layer of hyphae which seems to bear small hyaline globular conidia. Whether this is really genetically related to the perithecia or not is a question.... The perithecia when free break up in much the same manner as in *Fragosphaeria*, and the wall is of the same characteristic structure, and the spores brown. Fuckel's specimen is labelled on Oak."

The British material of *C. sulfurea* in the Broome Herbarium in the British Museum consists of two separate collections, that of October 1879 having young perithecia, some of which show suturing of the wall and all of which are embedded in the characteristic sulphur-coloured mycelium; and that of April 1876 having fully mature and often shattered perithecia with ascospores which measure from 4 to  $5.5 \times 2.5$  to  $3\mu$  (Text-fig. 1 G). The latter material is that from which



Text-fig. 1. Ascospores of species of *Cephalotheca*. A, *C. purpurea* (Shear's culture tube No. 4821). B, *C. purpurea* (Mason, No. 1228). C, *C. reniformis* (Mason, No. 1223). D, *C. reniformis* (Mason, No. 1167). E, *C. sulfurea* (Chesters, No. 4). F, *C. sulfurea* (Fungi Rhen. No. 2313). G, *C. sulfurea* (Berkeley & Broome, No. 1729). H-K, germinating ascospores (H, *C. sulfurea*; J, *C. reniformis*; K, *C. purpurea*).

the illustrations published in the *Annals and Magazine of Natural History* (Pl. XII, fig. 1) of 1878 were drawn ((i), p. 30). Berkeley and Broome observed the asci of this species but referred to them (*loc. cit.* p. 30) as "Sporangia"; in this they were followed by Cooke (*Grev. vi* (1878), 128).

The reference which Shear makes to "small hyaline globular conidia" associated with the sulphur-coloured mycelium about the peritheciun is of interest. Similar conidia are present in the specimen of *Fungi Rhenani*, No. 2313, in the British Museum. They measure  $3-4 \times 3\mu$  and occur in chains of two to several spores, but they have

not been observed attached to mycelium. They are present in considerable numbers in the British collection of Broome of 1879 which contains only immature perithecia. They are not present on the collection of W. B. Grove, but, as will be described later, they are formed on the mycelium produced from the germinated ascospores of this collection.

The collection of *C. sulfurea* from which monosporic cultures were obtained agrees precisely as regards the mycelium, perithecia and ascospores with the authentic material of the species and with the previous British collections. Further, conidia present upon authentic material and also on one previous British collection correspond exactly with those produced in culture.

(2) *C. reniformis* Sacc. & Therry

No authentic material of this species was available for examination and comparison, but all the collections of the fungus which have been made agree with the authors' description (*loc. cit.* p. 312), which may be translated thus:

"Perithecia gregarious, nestling among the cortical fibres or at length superficial, globose, mouthless but sometimes with a small apical papilla, later frequently collapsing and becoming cupulate, fuscous black in colour,  $\frac{1}{3}$ – $\frac{1}{4}$  mm. in diameter; at first clothed all over with filiform fuliginous hairs  $2\mu$  in diameter, afterwards becoming glabrous except at the base, with a somewhat thick, fuscous, small celled, parenchymatous texture; ascii either globose,  $10\mu$  in diameter, or ellipsoid  $15 \times 14$ – $12\mu$ , evanescent, eight-spored, ascospores conglobate, reniform,  $4$ – $5 \times 3$ – $3.5\mu$ , at first olivaceous, later becoming slightly fuliginous.

"Growing in the decorticated branches of decayed Poplar, Lyon, May 1880. Easily distinguished from other species by the small reniform ascospores."

The several collections of this species which I have examined and from which monosporic cultures have been obtained all exhibit small perithecia scattered throughout the decayed wood. On beech wood they are mainly clustered round the cavities left by the destruction of medullary ray tissue (Pl. XI, fig. 2), while on oak they are either dispersed throughout the wood or occur in dense masses in, and along, the walls of channels made by a boring beetle. Uncovered by any mycelial investment, the mature perithecia appear as black, shining spherical structures (Pl. XI, fig. 6),  $250$ – $350\mu$  in diameter, showing no obvious suturing of the carbonaceous wall. When shattered, the lower part of the wall usually remains intact as a cup within which lies the rather brown powdery mass of spores (Pl. XI, fig. 3). If the perithecia are slowly dried, the splitting of the wall can be observed to take place indiscriminately so that irregularly shaped areas from

the distal portion of the peritheciun are set free. The ascospores (Text-fig. 1 C and D), which are held together in clusters, are definitely reniform, light brown and  $4.5-5.0 \times 3.0-3.8 \mu$ . The perithecia, unlike those of *C. sulfurea*, are attached to the substratum by a mass of dark brown hyphae radiating from the base of the fruit body and penetrating into the wood.

The finding of this species upon beech at Richmond constitutes the first record of the species in Britain. Since then it has been observed on several occasions at Richmond and Birmingham. In every case the wood has been attacked by a boring beetle, and it is quite possible that the fungus is spread by the beetle.

(3) *C. purpurea* (Shear) comb.nov.

The collection of this species on dead beech at Richmond in 1932 represents its discovery in Britain and also the first field collection on the host plant. The material upon which the original description is based (Shear, *loc. cit.*) was obtained in culture as a contaminant of plates poured for the isolation of *Pilacre Petersii* from beech wood. The Richmond material bears both superficial and immersed perithecia, the latter being situated along the air spaces produced by the decay of the medullary rays. The wood is generally stained brown or brownish purple in the vicinity of the perithecia. These are dark in colour, usually black, and when mature show marked suturing of the wall (Pl. XI, fig. 4). Upon dry wood the majority of the perithecia are shattered (Pl. XI, fig. 7) to such an extent that only a flattened plate of loosely connected polygons of wall tissue remains. This may have a few ascospore clusters scattered over its surface (Pl. XI, fig. 5). Although the base of the peritheciun may be slightly embedded in a superficial mycelium or in the rotted wood, it is never definitely attached to the substratum as are the perithecia of *C. reniformis*. In this it resembles *C. sulfurea*. The collection on oak has younger perithecia, and these are separately covered by a weft of purple-coloured hyphae and the walls are also similarly tinted. The vestment of hyphae in this case is soft and not strictly comparable with the sulphureous villus of *C. sulfurea* where the individual hyphae are thickened and flexuose. The asci (*vide* Table I) are subglobose to globose (Text-fig. 1 B) and are arranged in clusters, and although they are evanescent the eight broadly bean-shaped ascospores (Text-fig. 1 B) remain grouped together even after the perithecial wall is shattered. The ascospores measure  $2.5-3.0 \times 1.5-2.0 \mu$  and are light brown in mass but individually more or less hyaline. By itself this species could legitimately be considered as perhaps belonging to the "Hyalosporeae" where in fact it is placed in Clements and Shear, *Genera of Fungi*.

Cultures of mature perithecia were sent to Dr Shear who was so good as to compare them with his type specimen (Pl. XII, fig. 2), and

also to send me a slide of perithecia and ascospores prepared from his type specimen (Pl. XII, fig. 3 and Text-fig. 1 A). He states that: "Your dried culture... I should say is undoubtedly our *F. purpurea*" (*in litt.*). As will be seen from Table I, there is no significant difference between the measurements of the American and British materials of this species. Referring to the generic status of *Cephalotheca sulfurea* and *Fragosphaeria purpurea* Dr Shear states (*in litt.*) that: "At present, I am inclined to think that so far as the genera are concerned they are the same...."

Table I. Measurements of perithecia and spores of species of *Cephalotheca*.

Specimens examined	Perithecia	Asci
<i>C. sulfurea</i> :		
(1) Exsicc. Fung. Rhen. No. 2313	330-500 $\mu$	10 $\mu$ diam.
(2) Exsicc. Berkeley and Broome No. 1729, in Herb. Brit. Mus.	—	—
(3) Exsicc. Chesters No. 4	250-500 $\mu$	8-11 $\mu$ diam.
<i>C. reniformis</i> :		
(1) Measurements from <i>Syll.</i> 1, p. 37	250-330 $\mu$	15 $\times$ 14-12 or 10 $\mu$ diam.
(2) Exsicc. Mason No. 1167	250-350 $\mu$	11 $\times$ 8-10 or 10-11 $\mu$ diam.
<i>C. purpurea</i> :		
(1) Measurements from Shear ( <i>loc. cit.</i> p. 124)	—	4-6 $\mu$ diam.
(2) Exsicc. Mason No. 1228	300-350 $\mu$	5.0-6.5 $\mu$ diam.
Specimens examined	Ascospores	Conidia
<i>C. sulfurea</i> :		
(1) Exsicc. Fung. Rhen. No. 2313	4-6 $\times$ 3-4 $\mu$	3-4 $\times$ 3 $\mu$
(2) Exsicc. Berkeley and Broome No. 1729, in Herb. Brit. Mus.	4-4.5 $\times$ 2.5-3 $\mu$	3-4 $\times$ 2.0-2.5 $\mu$
(3) Exsicc. Chesters No. 4	4.5-6 $\times$ 3-4 $\mu$ , mostly 6 $\times$ 4 $\mu$	4.5-5 $\times$ 2-3 $\mu$ (cultures)
<i>C. reniformis</i> :		
(1) Measurements from <i>Syll.</i> 1, p. 37	4-5 $\times$ 3.0-3.5 $\mu$	—
(2) Exsicc. Mason No. 1167	4.5-5 $\times$ 3.0-3.8 $\mu$	4-5 $\times$ 1.5-2 $\mu$ (cultures)
<i>C. purpurea</i> :		
(1) Measurements from Shear ( <i>loc. cit.</i> p. 124)	2.25-2.75 $\times$ 1.5-2 $\mu$	3-4 $\times$ 1.0-1.5 $\mu$
(2) Exsicc. Mason No. 1228	2.5-3.0 $\times$ 1.5-2 $\mu$	3-4 $\times$ 1.0-1.5 $\mu$

The comparisons made in the foregoing pages appear to me to indicate that the species under investigation can be identified with previous descriptions and material of three species, two of which are already recognised as belonging to *Cephalotheca*. The life histories of the three species will indicate similarities which necessitate their common treatment in a single genus.

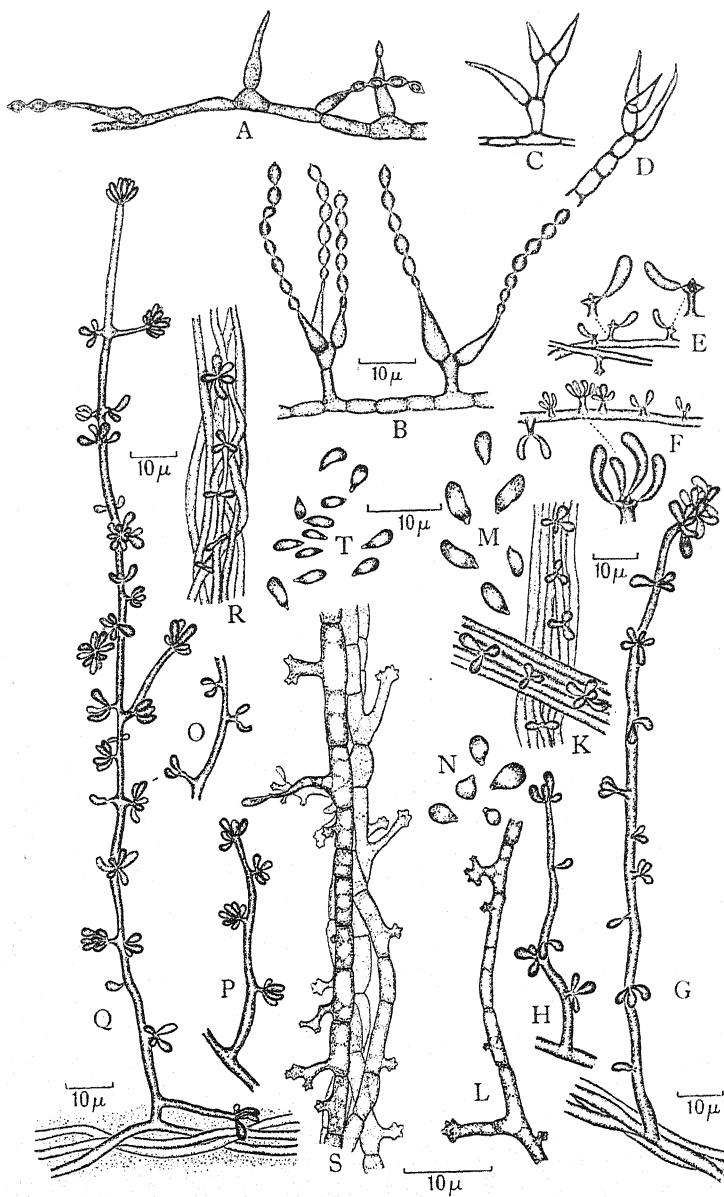
## III. THE LIFE HISTORIES

(a) *The conidial stage*

The freshly discharged ascospores germinated easily on a variety of media, but the species show marked differences in the optimum temperature for germination. Those of *C. sulfurea* have an optimum temperature between 16 and 18° C., those of *C. reniformis* between 20 and 26° C., and those of *C. purpurea* between 22 and 26° C. In each case the germ tubes are produced from the poles of the spore (Text-fig. 1 H-K) and the first lateral branch is formed near to the ascospore. Conidia are developed within two to four days after germination. The conidial stage appears earliest in *C. purpurea* and latest in *C. sulfurea*. In each species the first conidia are borne upon conidiophores which are simpler than those present on mature mycelium.

(1) *C. sulfurea*.

The conidia are formed on simple, erect, unicellular branches which are at first of an even thickness throughout their length, but during growth the apical part becomes attenuated and the whole forms a simple flask-shaped cell (Text-fig. 2 A). The first spore is formed as a distal swelling which remains in open communication with the hypha until a second, and lower, spore is differentiated. The wall between the two spores now contracts so that the protoplasmic continuity is severed and a small bridge of wall material separates the two spores. This basipetal formation is repeated and a chain of spores of some considerable length is produced (Text-fig. 2 B). The flask-shaped conidiophore must be regarded as a phialide producing serial phialospores<sup>(6)</sup> which for a time remain in contact with one another. The conidia are liberated either in units or in small linear series; they never collapse into a sticky mass. The conidia are small, uninucleate, ovate structures (*vide* Table I) which germinate easily upon a variety of media or in tap water. Simple phialides occur on the young mycelium and on aerial parts of the old mycelium, but the surface plexus of hyphae produces more complex structures (Text-fig. 2 B) which may be immersed, and are reminiscent of a rather lax penicilliod growth. On these the phialides arise from branches which may be one or more cells in height (Text-fig. 2 B-D), with an apical group of two or more phialides and lateral phialides, either singly or in groups, throughout their length (Text-fig. 2 C). The very considerable, widespread spore production gives the adult mycelium a white or yellowish powdery appearance. The colour varies on different media and at different temperatures. It is most intense on oat agar containing sucrose at 18° C. No pigmentation of the medium occurs.



Text-fig. 2. A-D, phialides and phialospores of *C. sulfurea*. E-N, fertile hyphae and radulospores of *C. reniformis*. O-T, fertile hyphae and radulospores of *C. purpurea*. For further explanation see text.

(2) *C. reniformis*.

The conidia, which are falcate and  $4-5 \times 1.5-2\mu$  in size (Text-fig. 2 M), are always borne upon minute papillate processes (Text-fig. 2 E). In their simplest form these arise singly on the cells of the superficial and aerial mycelium (Text-fig. 2 G and H); in their most complex form they are arranged in masses over the ends of swollen lateral projections (Text-fig. 2 F-L). A septum may very occasionally occur at the base of these projections, thus forming a simple unicellular conidiophore. In this latter case a definite spiral arrangement can be traced in the order of production of the papillae (Text-fig. 2 K and L). This type of spore formation was differentiated among others as a "radula\*" spore form" by Mason (6). In the present state of our knowledge it would be unwise to compare directly this spore form with the phialospores of *C. sulfurea*. A relevant case may be cited from *Botrytis cinerea*, where the "Botrytis" spore is a higher development of the radula spore type shown by *C. reniformis*, and phialospores comparable to the conidia of *C. sulfurea* are represented by the so-called microconidia. On most agar media the mycelium of *C. reniformis* consists of a matted surface growth of interwoven strands of hyphae producing abundant conidia which give the mycelium a somewhat waxy appearance and cream-like colour. As the medium dries out, or upon hard agar or wood, superficial rope-like strands develop which bear upright fertile hyphae of varying length (Text-fig. 2 G and H). This type is floccose in appearance.

(3) *C. purpurea*.

The conidial condition of this species was described by Shear (*loc. cit.* p. 124) as: "Thin, white, effuse, much branched; conidia formed on somewhat enlarged, elongated, and roughened ends of the alternately branched fertile hyphae (Pl. XII, fig. 4), oblong-elliptic, in-equilateral or suballantoid, non-septate, hyaline,  $3-4 \times 1-1.5\mu$ ." The fertile hyphae of isolations from British material only occasionally branch in a regularly alternate manner (Text-fig. 2 P). The branching of large fertile hyphae is very irregular (Text-fig. 2 Q). The genesis of the individual conidium (Text-fig. 2 O-S) is precisely similar to that of *C. reniformis*, and though somewhat smaller (see Table I), it has the same shape (Text-fig. 2 T). The cultures are more flocculent than those of *C. reniformis*, due to the more extensive development of aerial mycelium. On microscopic characters alone it would be impossible to differentiate the conidial stage of *C. purpurea* from that of *C. reniformis*. The macroscopic appearance of the cultures is certainly different in a degree, but not to such an extent as would allow one without previous knowledge of the perithecia connected with each species to consider them specifically distinct.

\* *radula* (Latin)=nutmeg grater.

## (b) The ascophorous stage

Perithecia are only abundant when the factors which influence the growth of each species are at their optimum value. Of these factors the composition of the medium, the humidity of the atmosphere and the temperature are the most important, provided that the reaction of the medium falls within pH 6.0-7.0. The most favourable media are maize or oat paste agar and 2 per cent. malt agar. Synthetic media containing not less than M/250 maltose and NaNO<sub>3</sub> or KNO<sub>3</sub> as the source of nitrogen support the formation of perithecia by *C. reniformis* and *C. purpurea* but not by *C. sulfurea*. Maltose is a better source of carbohydrate than sucrose.

Perithecia of *C. reniformis* and *C. purpurea* develop abundantly upon fresh, autoclaved wood of beech, oak and ash, but only sparsely upon rotted specimens of these woods or specimens which have been subject to water extraction and partial chlorination. It is difficult to develop the perithecia of *C. sulfurea* either on fresh or rotted wood. The optimum range of atmospheric humidity lies between one-eighth and five-eights of full saturation, and perithecia are usually more plentiful in drier conditions. A very clear optimum range of temperature exists for each species. Linear growth of *C. sulfurea*, though never extensive, is greater between 16 and 18° C., and is negligible at 24° C. Perithecia have so far only been developed upon hard malt agar and oat paste agar between 16 and 18° C. with an air humidity of one-eighth to one-quarter saturation. The relative linear growth and perithecial formation of *C. reniformis* and *C. purpurea* is given in Table II, which shows that the optimum temperature for the former is slightly lower than for the latter. This is quite independent of the medium used.

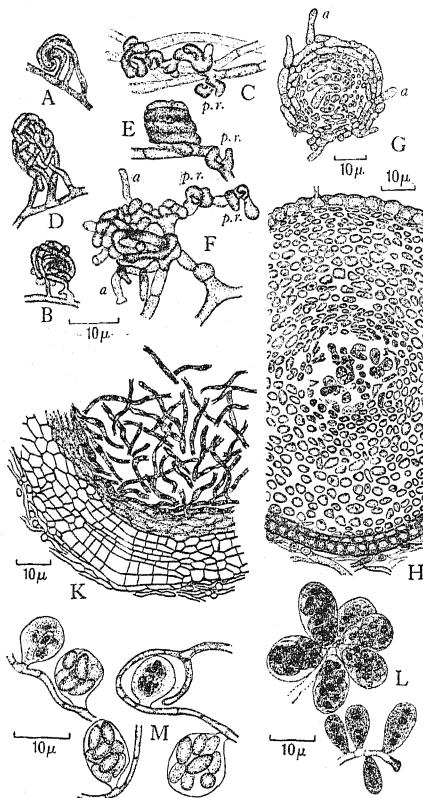
Table II

Temperature (malt agar)	Linear growth as a % of the optimum value		Relative abundance of perithecia	
	<i>reniformis</i>	<i>purpurea</i>	<i>reniformis</i>	<i>purpurea</i>
13	68	50	+	0
19	100	87	+++	+++
24	99	100	++	+++
29	85	99	0	++

+=few perithecia; +++=abundant perithecia.

The perithecial rudiments of the three species are similar and consist of two (Text-fig. 3 C) or, sometimes, three (Text-fig. 3 A) small upright branches which coil loosely round one another to produce an irregular or spherical structure (Text-fig. 3 B-F). They are scattered over the surface mycelium of *C. reniformis* and among the aerial hyphae as well in *C. sulfurea* and *C. purpurea*. As yet it is impossible to say whether the fundaments should be regarded as func-

tional sexual organs. No fusion has been observed between the coiled hyphae. These of *C. reniformis* and *C. purpurea* (Text-fig. 3 A, B, D) are similar and differ in their more delicate construction from those of *C. sulfurea* (Text-fig. 3 C, E, F). The coiled hyphae soon become surrounded by branching filaments which arise from their base (Text-



Text-fig. 3. Stages in the development of the perithecia of *C. purpurea* (A and D), *C. reniformis* (B) and *C. sulfurea* (C, E and F). G, longitudinal section through a young perithecium of *C. reniformis* showing the central spiral hypha and young attachment hyphae (a). H, an older perithecium of *C. reniformis* showing the central ascogenous hyphae. K, a sector of the perithecium of *C. sulfurea* showing the loosely woven ascogenous hyphae. L, asci of *C. reniformis*. M, asci of *C. sulfurea*.

fig. 3 B, D). These sterile filaments form the wall of the perithecium and soon become brown. Thus the perithecium is entirely derived from the further growth of two or three fundamental hyphae. At this time, when the outer wall layers are first clearly defined, the perithecium of each species is similar in appearance (Text-fig. 3 G). A double layer of brown, thick-walled cells surrounds a mass of inter-

woven hyphae, in the centre of which lies a single spiral hypha in whose dense finely granular protoplasm prominent nuclei are embedded. The examination of numerous perithecia which were cleared and then stained in erythrosin indicates definitely that only a single hypha is concerned. Subsequent development varies according to the species.

(1) *C. reniformis*.

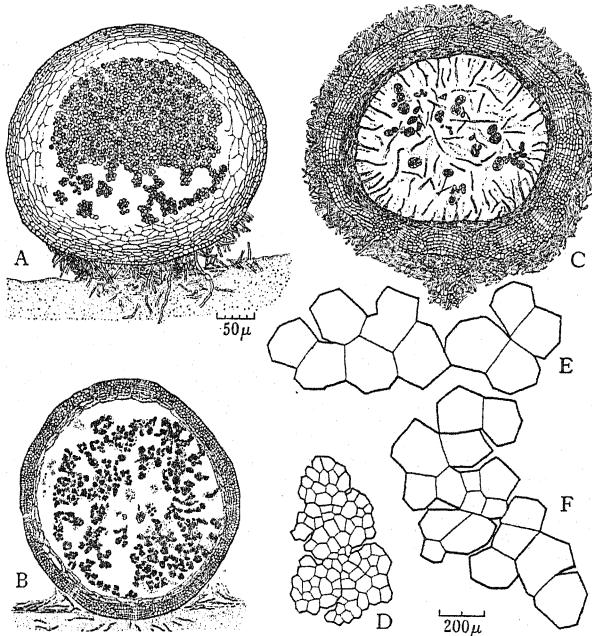
As the perithecium grows, a spherical mass of hyaline pseudoparenchymatous tissue is formed within the dark brown or black wall layers. In the centre of this lie a number of hyphae which stain deeply and often contain paired nuclei (Text-fig. 3 H). They are ascogenous hyphae and are derived from the original spiral hyphae. Increasing in number they become interpolated between the cells of the ground tissue which is ultimately destroyed except for a thin zone adjacent to the outer indurated wall. During this the development of clusters of asci at the apices of the ascogenous hyphae (Text-fig. 3 L) begins and continues until the centre of the perithecium is almost completely filled. The asci are spherical or elliptical, and, being entirely occupied by ascospores, appear sessile. They are evanescent and cannot usually be found in shattered perithecia. They may even have disappeared before normal rupture of the perithecial wall occurs. The eight ascospores are definitely reniform from the time the spore wall is formed, and though at first hyaline they gradually become olive brown and finally fuliginous.

The mature perithecium (Text-fig. 4 A) is a spherical, black, glabrous structure firmly attached to the substratum by brown thick-walled hyphae which are produced at an early stage in development as outgrowths from the hyphae forming the wall (Text-fig. 3 G, a). This is about three to five cells in thickness, and in surface view appears to consist of small regular plates (Text-fig. 4 D) of indurated cells separated by a network of thinner walled elements which tear when the perithecium ruptures. As the perithecium dries, and prior to the actual fragmentation, the apical portion generally collapses to form a cup-shaped depression. This was noted by Saccardo in his diagnosis of the species. An apical cap may then be forced off or the whole perithecium may gape in an irregularly two-lipped manner. The basal attached portion usually remains as a cup and is filled with a brown powdery mass of ascospores.

(2) *C. purpurea*.

In this species the development of the ascogenous hyphae and asci (Text-fig. 3 L) is similar to that in *C. reniformis*, except that the asci are smaller and more numerous. The ascospores are bean-shaped, and though ultimately yellowish they remain hyaline for a consider-

able period. The wall of the mature perithecium (Text-fig. 4 B) is from three to four cells in depth. The sutures dividing the wall into polygonal plates (Text-fig. 4 E) have already been referred to (*vide* p. 266). They are built up of tangentially elongated elements whose central cells are not thickened (Text-fig. 5 G). These cells form an almost straight line along which cleavage occurs when the perithecium explodes after drying. This liberates most of the polygonal



Text-fig. 4. Longitudinal sections through the perithecia of: A, *C. reniformis*. B, *C. purpurea*. C, *C. sulfurea*. Segments of the perithecial wall of D, *C. reniformis*. E, *C. purpurea*. F, *C. sulfurea*. (D-F drawn to the same scale with fine lines representing the position of sutures.)

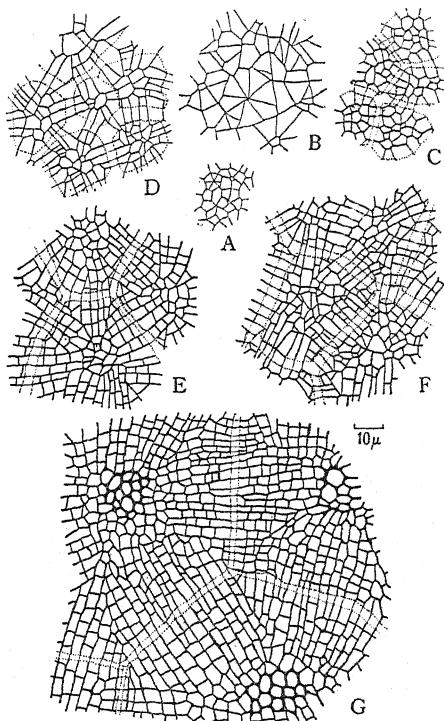
plates in the form of a flat disc of disjointed segments. The majority of the ascospores are dispersed by the explosion, but some remain in groups over the centre of the disc.

The young perithecia of this species seem to be invested by a purple villus. This is due to a pigment developed in the cells of the hyphae in the region of the perithecia and occurs characteristically in cultures exposed to daylight. The villus is not an integral part of each individual perithecium which produces only a few simple attachment hyphae. These seldom persist to maturity. That the purple pigment diffuses into the medium was noted by Shear (*loc. cit.* p. 125) who also

stated that the perithecia are dark purple. I have only occasionally observed this in cultures, and in field collections only that from oak possessed perithecia with definitely pigmented walls.

(3) *C. sulfurea*.

In *C. sulfurea* the ascogenous hyphae occupy practically the whole space within the perithecial wall (Text-fig. 3 K). There is only a thin layer of pseudoparenchymatous tissue lining the wall. The asci first appear towards the centre of the peritheciun and are arranged at



Text-fig. 5. Stages in the development of sutures in the perithecia of *C. sulfurea* (A, C, E), *C. reniformis* (B, D, F) and *C. purpurea* (G). (Figures F and G are drawn from mature shattered perithecia but figure E is drawn from a young perithecium. All figures drawn to the same scale).

intervals along the ascogenous hyphae (Text-fig. 3 M). The almost mature peritheciun (Text-fig. 4 C) has a relatively wide wall in which suture lines are clearly defined by layers of tangentially elongated thin-walled cells, in a manner similar to those of *C. purpurea* (Text-fig. 5 E). The whole peritheciun is covered at this stage by a mass of interwoven, flexuose, thick-walled and sulphur-coloured

hyphae among which occur ordinary hyphae bearing conidia. The sulphur colour may be absent when the perithecia are grown in darkness, but it soon appears on exposure to light. At this time the ascogenous hyphae with their asci are still visible, but as the perithecium matures the former disorganise and only the younger of the latter remain intact, so that the perithecium is filled with clusters of ovoid, brown ascospores among which are a few eight-spored asci. As the perithecium enlarges, its apex becomes glabrous, while its base remains embedded in the mass of sulphur-coloured hyphae. Since the perithecia are formed in clusters, this sulphureous villus is very conspicuous both upon agar media and upon wood. When the perithecium shatters the wall breaks down along the suture lines, discharging the apical series of plates and leaving a basal cup of partially separated plates enclosing the spores.

The presence of definite suture lines in the perithecial wall of the three species of *Cephalotheca* is an important diagnostic character. Whether these sutures are visible, under low-power magnification, on the wall of the perithecium (as in *C. sulfurea* and *C. purpurea*) or not (as in *C. reniformis*) their presence can be demonstrated by suitable preparation. A comparison of their development in the three species shows that in each they are formed by the further growth of certain prismatic or triangular cells (Text-fig. 5 A, B) grouped round a polygonal central cell. The prismatic cells become elongated, and by transverse division (Text-fig. 5 C, D) produce radiating lamellae of thick-walled cells (Text-fig. 5 E, F, G). The central cell gives rise to an indurated plate of cells (Text-fig. 5 G). One or more cells, midway between the lamellae belonging to different plates, remain thin-walled and may represent meristematic cells. Collectively they represent the lines of suture along which the perithecium ruptures. These developmental stages, when considered along with other perithecial characters, indicate a close relationship between the three species.

#### IV. DISCUSSION

##### (a) *The conidial stage*

Considering these three species on the evidence presented in this paper, it appears that the conidia described for *C. reniformis* and *C. purpurea* are homologous and fundamentally differ from the conidia described for *C. sulfurea*. I am of the opinion that a phialospore stage of *C. reniformis* and *C. purpurea* homologous with that of *C. sulfurea*—the type species of the genus—may yet be found.

##### (b) *The ascophorous stage*

The perithecial rudiments of *C. reniformis* and *C. purpurea* are of similar construction and differ only in size from those of *C. sulfurea*.

In the further differentiation of the perithecium, and particularly of the asci, *C. reniformis* and *C. purpurea* exhibit a closely parallel development which differs only in degree from that of *C. sulfurea*. According to Fuckel the diagnostic characters of the mature astomous perithecium are chiefly the fragile nature of the wall and the clustered arrangement of the asci at the ends of branched ascophorous hyphae. Von Höhnel<sup>(4)</sup> stated that besides being fragile the perithecia break up along characteristic sutures. The present investigation shows that the sutures in the wall of the perithecium of *C. purpurea* are precisely similar in structure and development to those in the perithecium of *C. sulfurea*. After emending the diagnosis to include von Höhnel's observation, and bearing in mind that *C. sulfurea* is taken as the type species, the only conclusion which can be drawn from the sum of the evidence presented here is that the three species should be generically related.

The coiled fundaments of the perithecium of the species described here are similar to those described by Brefeld for his *Penicillium glaucum* (*Carpenteles asperum* (Langeron) Shear<sup>(9)</sup>). The formation of the asci upon the ascogenous hyphae may be compared with that described for the *Aspergillus herbariorum* group or for *Penicillium Brefeldianum*<sup>(2)</sup>. There is every reason to believe that *Cephalotheca* should be placed in relation to these genera and that it should be distinguished from them by the specialisation of the perithecium in regard to the liberation of the ascospores.

#### (c) *Synonymy*

The synonymy of *C. sulfurea* has been discussed by von Höhnel<sup>(5)</sup>. He reviewed the position with regard to two species previously classified as Sphaeropsids and stated that *Aposphaeriopsis fusco-atra* Died. was *C. sulfurea*. He hazarded the view that *Fairmania singularis* Sacc. might be *C. sulfurea* and indicated that he thought *C. reniformis* merely a synonym for *C. sulfurea*. Petrak and Sydow<sup>(8)</sup>, after comparing the type specimen of *Fairmania singularis* in Saccardo's herbarium with *C. sulfurea*, stated that they consider them synonymous. These reports indicate that the two Sphaeropsids should be regarded as species of *Cephalotheca*. Having had the advantage of studying a fungus which closely agrees with the description of *C. reniformis*, I am certain that this species is not synonymous with *C. sulfurea*. The latter has a sulphur-coloured villus surrounding the perithecium and ovoid ascospores measuring  $6 \times 4\mu$ . *C. reniformis* has a glabrous perithecium and reniform ascospores measuring  $4-5 \times 3-3.8\mu$ . Diederke describes *Aposphaeriopsis fusco-atra* with a glabrous fructification (200-250 $\mu$  in diameter) containing spores measuring 4-5 $\mu$  in diameter which are drawn as reniform (Pl. XII, fig. 5). These characters indicate that it is *C. reniformis* and not *C. sulfurea*. The spores of

*Fairmania singularis* are described as (Saccardo, *loc. cit.* p. 276): "Solae calcaneum exakte imitantis" (exactly like the heel of a slipper). At first hyaline, they later become sooty and measure  $5.7\mu$  in diameter. Since Petrak and Sydow consider *Fairmania singularis* a good *Cephalotheca*, these characters indicate that it should be held synonymous with *C. reniformis*.

## V. SUMMARY

### A. Diagnosis of Cephalotheca

1. *Perithecia* astomous, simple, spherical, carbonaceous, fracturing at maturity along well-defined sutures; young *perithecia* sometimes covered by a coloured villus, in other species totally glabrous; on dry decayed wood, superficial or semi-immersed and free, or immersed and attached basally. *Asci* spherical or elliptical, on branched ascogenous hyphae, alternate or clustered, more or less sessile, eight-spored, evanescent. *Ascospores* conglobate, ovate or bean-shaped or reniform, continuous, hyaline to yellow or fuscous (light to dark brown in mass).

2. *Conidia* formed upon a white or slightly coloured mycelium. *Conidia* hyaline, continuous, either serial phialospores, ovate or broadly elliptical, or radulospores, falcate or suballantoid.

Type species: *C. sulfurea*.

### B. Key to the accepted species of Cephalotheca

(a) *Ascospores* *ovate*.

*Perithecia* surrounded by a sulphureous villus.

*Ascospores*  $6 \times 4\mu$ . *Phialospores*  $3-5 \times 2-3\mu$ .

*C. sulfurea*.

(b) *Ascospores*  $\pm$  *reniform*.

(i) *Perithecia* partly invested with a transitory purple coloured villus. *Ascospores* bean-shaped  $2.3-3.0 \times 1.5-2.0\mu$ . *Radulospores*  $3-4 \times 1.5\mu$ .

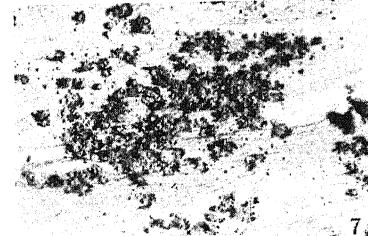
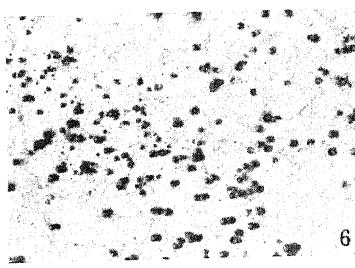
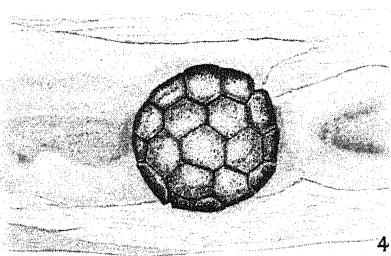
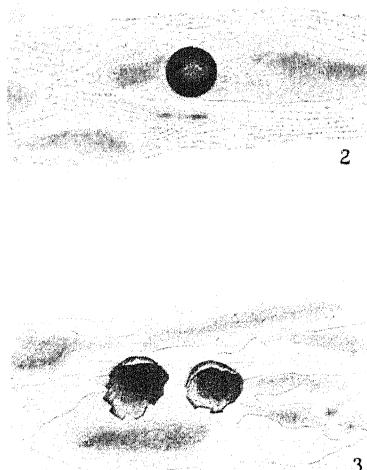
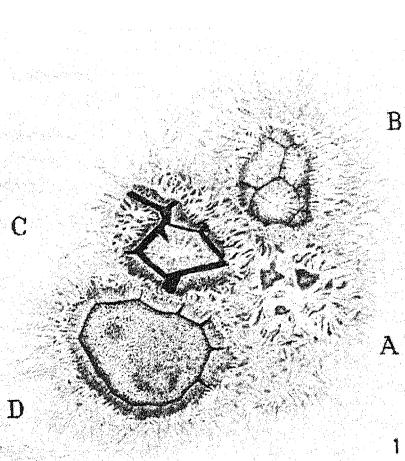
*C. purpurea*.

(ii) *Perithecia* totally glabrous, attached basally to the substratum.

*Ascospores* reniform  $4-5 \times 3.0-3.8\mu$ . *Radulospores*  $4-5 \times 1.5\mu$ .

*C. reniformis*.

I desire to express my gratitude to Mr E. W. Mason, of the Imperial Mycological Institute, Kew, not only for suggesting this investigation and for providing material but also for his continued help and criticism throughout its course. The kind assistance of Dr C. L. Shear, of Washington, U.S.A., made it possible to place the type species of *Fragosphaeria* exactly. To Mr W. B. Grove, of Birmingham, I am deeply indebted for the collection of *C. sulfurea* which rendered a thorough comparison between the type species of the two genera





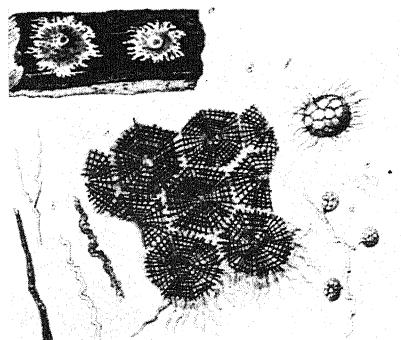


Fig. 1

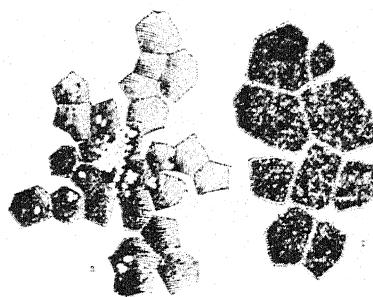


Fig. 2



Fig. 3

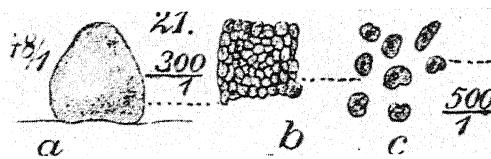


Fig. 5

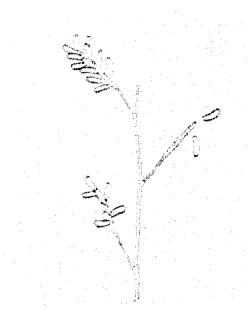
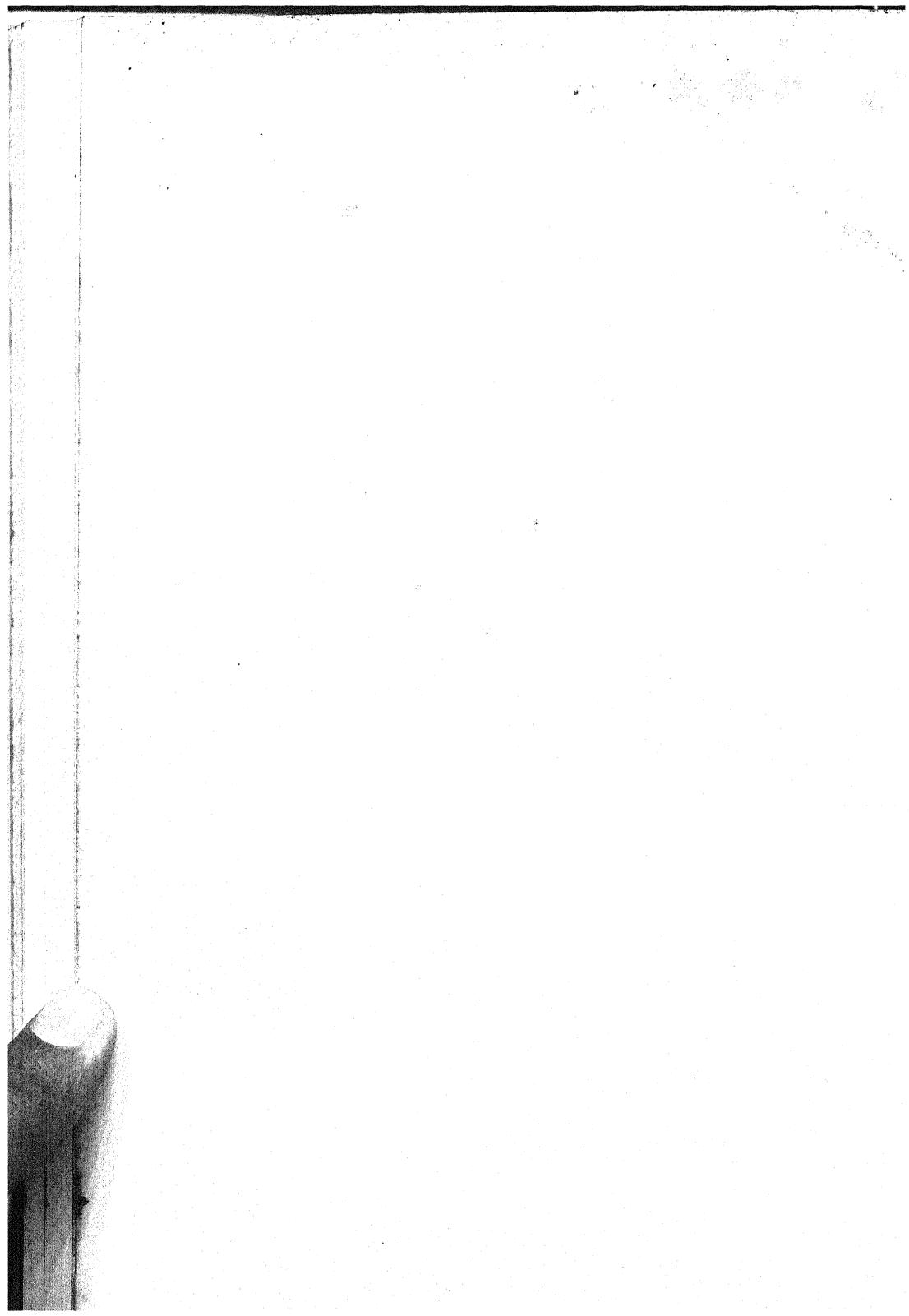


Fig. 4



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possible. My thanks are also due to Mr J. Ramsbottom and Miss E. M. Wakefield for affording facilities for the inspection of Herbarium material.

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### EXPLANATION OF PLATES XI AND XII

#### PLATE XI

Fig. 1. Perithecia of *Cephalotheca sulfurea* in various stages of development.  
Fig. 2. Mature perithecium of *C. reniformis* on beech wood.  
Fig. 3. Shattered perithecia of *C. reniformis*.  
Fig. 4. Mature perithecium of *C. purpurea* showing suturing.  
Fig. 5. Shattered perithecium of *C. purpurea* showing clustered groups of ascospores.  
Fig. 6. Perithecia of *C. reniformis* developed on a culture of beech wood.  
Fig. 7. Perithecia of *C. purpurea* on a similar culture.

#### PLATE XII

Reproductions of drawings of species of *Cephalotheca*.  
Fig. 1. *C. sulfurea* (Berkeley and Broome, 1878).  
Figs. 2-4. *C. purpurea* (Shear, 1923).  
Fig. 5. *Aposphaeriopsis fuscocatra* (Diedicke, 1913).  
For further explanation see text.

While this paper was in press an extensive collection of *Cephalotheca sulfurea* was made at Birmingham on structural timber which had been covered by ashes. The mycelium bore both phialospores and mature perithecia. There now seems to be little doubt that this species is a "domestic mould" occurring superficially upon a variety of woods.

## THE FUNGI OF WICKEN FEN, CAMBRIDGESHIRE

By E. J. H. CORNER, M.A.

THIS preliminary list of about 250 fungi includes most of the common species which are to be found each year on the Fen and several which are interesting either for their rarity or their unusual occurrence; yet it is far from complete. I visited the Fen during the years 1924-8 and at most seasons except the early autumn, and collected chiefly the Basidiomycetes, the list of which is fairly representative. That of the Ascomycetes is meagre, however, because of the difficulty of identification, though, in fact, as Pyrenomycetes and inoperculate Discomycetes, they are exceedingly abundant. Neither Fungi Imperfecti nor Mycetozoa were collected. Probably no less than 700 species of fungi will be found on the Fen.

The absence of woodland precludes the occurrence of most species with large fruit bodies, so that even in autumn fungi are not obvious and must be looked for. But the Fen offers the mycologist two interesting habitats. Under the willow and alder are low mounds of earth, bare or but thinly covered with fallen leaves and, in places, with rotting clumps of sedges which have died in the shade: this earth is dark, rich, friable and light in weight, and consists almost entirely of vegetable remains comminuted and voided by woodlice. Here the larger toadstools occur, such as *Inocybe*, *Leptonia*, *Mycena*, *Psathyra*, *Psathyrella*, *Russula violacea*, *Hygrophorus conicus*, *Tricholoma melaleucum*, *Naucoria escharoides*, and the terricolous Discomycetes *Aleuria*, *Galactinia*, *Ciliaria*, *Pulvinula*, and *Sepultaria*: on the dead stumps and branches occur the lignicolous species of *Polyporus*, *Stereum*, *Corticium*, etc. Then, in the Fen itself, the remains of herbaceous plants and the tussocks of dead matted leaves of grasses and sedges support the smaller Basidiomycetes and microfungi in such vast numbers that the air is dusty with their spores. *Marasmius ramealis* and *Omphalia integrilla* develop in troops indiscriminately on these remains; *Androsaceus graminum*, *Coprinus Friesii* and *Pistillina Patouillardii* have a preference for the haulms of *Phragmites*, and *Marasmius Menieri*, *Omphalia gibba* and *Pistillaria aculeata* for the leaf-bases of *Cladium Mariscus*. *Psathyra Typhae* grows on the dead haulms of *Phragmites* and *Scirpus* standing in water and, like *Coprinus Friesii*, the fruit-bodies develop even at the water's surface. *Omphalia candida* is found only on the dead leaf-bases of *Sympyrum officinale*, although on turning aside the living leaves between July and October it can be seen that nearly every plant is infected. These Basidiomycetes fruit generally in late summer and

autumn. In the spring and early summer and again in autumn, to a lesser extent at other times of the year, inoperculate Discomycetes of the genera *Mollisia*, *Helotium*, *Dasyphypha*, etc., cover the herbaceous remains with their minute apothecia in profuse variety, and Pyrenomyces, though less conspicuous, are even more abundant. Both habitats are ideal for the growth of fungi: vegetable remains abound and soil and air are almost continuously damp and little disturbed by the winds. The fungi rot the dead plants, turning them into living spores which floating round settle down as manna for the microscopic animals.

In the early summer the fruit-bodies of *Mitrula sclerotipus* and *Claviceps microcephala* develop in great numbers throughout the Fen, the one on the dead stems of grasses and the other on the dead inflorescences particularly of *Phragmites*: the aecidial stage of *Puccinia coronata* becomes almost epidemic on the buckthorn, rendering the bushes most unsightly. In midsummer, *Melampsorella Symphyti* covers the underside of the leaves of *Symphytum officinale* with an orange powder of uredospores. In autumn *Typhula phacorrhiza* takes the place of *Mitrula sclerotipus*, its thread-like fruit-bodies forming miniature forests, and *Pistillina Patouillardii* swarms over the dead remains of *Phragmites*. It may be that the sclerotial species of *Mitrula* and *Typhula*, like *Claviceps* and *Sclerotinia*, have special life histories.

Remarkable is the presence of the underground puffball, *Hymenogaster tener*, which generally grows in the deep humus of beechwoods. It is in the carr on the east of the Burwell end of the main drove.

As rarities only *Puccinia bullata*, which is confined to its rare host *Peucedanum palustre*, and *Pistillina hyalina* can be reckoned. *P. hyalina* I found once, in February 1925, on a dead grass stem half-way along the main drove: it is a unique species hitherto known only from Quélet's original gathering in France some fifty years ago, and worthy of a distinct genus. There is also a second species of *Mitrula* with a minute sclerotium and very slender light brown fruit-bodies, which develop in June among the rushes; it is certainly new to science.

*Marasmius Menieri*, *Psathyra Typhae*, *Pistillaria aculina* and *P. aculeata* are recorded here for the first time for Great Britain, and the recent records of *Omphalia candida*, *O. gibba*, *Pistillina hyalina* and *P. Patouillardii* are from Wicken Fen and district. Apart from *P. hyalina*, all are fairly common and widespread in such localities. But many strange fungi and rarities are to be discovered in the fens. The species of *Pistillaria*, particularly those on herbaceous remains, are little known and would repay study; and one should look also for aquatic fungi, Laboulbeniaceae and other entomogenous groups.

The nomenclature adopted in this list is that of the standard works cited in the bibliography, and in their sense the species have been taken. As regards the newly recorded species, I have appended with

a few critical notes descriptions from material collected on the Fen.

In conclusion, I must express my indebtedness to Mr Carleton Rea for his invaluable assistance in revising the manuscript and kindly confirming the more difficult identifications.

## BASIDIOMYCETES

### HOMOBASIDIAE

*Acia denticulata* (Pers.) Bourd. & Galz., *uda* (Fr.) Bourd. & Galz.  
*Androsaceus graminum* (Lib.) Pat.  
*Annellaria separata* (L.) Karst., on horse-dung with other coprophilous species.  
*Bolbitius vitellinus* (Pers.) Fr., in the grass by the main drove.  
*Claudopus byssisedus* (Pers.) Fr., on earth, stems, mosses, etc., *variabilis* (Pers.) W. G. Sm.  
*Clavaria tenuipes* B. & Br., common on sticks and bare ground in the fen.  
*Coprinus cordisporus* Gibbs, *ephemerus* (Bull.) Fr., *Friesii* Quél., common on *Phragmites*, *Cladium*, etc., *niveus* (Pers.) Fr., *plicatilis* (Curt.) Fr.  
*Corticium confluens* Fr., *flavescens* (Bon.) Mass., *Sambuci* (Pers.) Fr.  
*Cortinarius flexipes* Fr., in the carr.  
*Cyphella capula* (Holmsk.) Fr., *capula* var. *flavescens* Pat., *lactea* Bres., common on dead grass leaves.  
*Eccilia griseo-rubella* (Lasch) Fr.  
*Epithele Typhae* (Pers.) Pat., common.  
*Galera hypnorum* (Schrank) Fr., *tenera* (Schaeff.) Fr.  
*Grandimia mutabilis* (Pers.) Bourd. & Galz.  
*Hygrophorus conicus* (Scop.) Fr.  
*Hymenogaster tener* Berk.  
*Hypoloma appendiculatum* (Bull.) Fr., especially where scrub had been cut down and sticks heaped.  
*Hypochnus fuscus* (Pers.) Fr., *granulosus* (Peck) Burt., *roseo-griseus* Wakef. & Pears., on dead *Cladium* leaves.  
*Inocybe geophylla* (Sow.) Fr., under bushes, *geophylla* var. *fulva* Pat., on the ground in the sedge-fen, *rimosa* (Bull.) Fr., *sensu* Rea.  
*Irpea obliquus* (Schrad.) Fr.  
*Leptonia asprella* Fr., *sericella* (Fr.) Quél., *serrulata* (Pers.) Fr. var. *laevipes* Maire.  
*Marasmius Menieri* Boud. (see description at the end of list), *ramealis* (Bull.) Fr.  
*Mycena acicula* (Schaeff.) Fr., *corticola* (Schum.) Fr., *filopes* (Bull.) Fr., *metata* Fr., *vitilis* Fr.  
*Naucoria cerodes* Fr., *effugiens* Quél., *escharoides* Fr., *graminicola* (Nees) Fr.  
*Omphalia candida* Bres., only on *Sympyton officinale*, *gibba* Pat., common on *Cladium*, rarely on willow leaves, *gracilis* Quél., *grisea* Fr., *integrella* (Pers.) Fr., common on dead twigs, leaves, haulms, etc., *muralis* (Sow.) Fr., *stellata* Fr.  
*Panaeolus campanulatus* (L.) Fr., *papilionaceus* (Bull.) Fr., *sphinctrinus* Fr.  
*Peniophora cinerea* (Fr.) Cke., *detricta*, Bourd., forming large patches on dead leaves of *Cladium*, *incarnata* (Pers.) Cke., *longispora* (Pat.) v. Hoehn. & Litsch., frequent on sticks and haulms.  
*Pistillaria aculeata* Pat. (see description at end of list), *aculina* (Quél.) Pat. (see description at end of list), *micans* (Pers.) Fr., *pusilla* (Pers.) Fr., *uncialis* (Grev.) Cost. & Dufour, on dead herbaceous stems.  
*Pistillina hyalina* Quél., *Patouillardii* Quél.  
*Pluteus hispidulus* Fr. (see description at end of list), *nanus* (Pers.) Fr. var. *lutescens* Fr., on sticks and *Phragmites* stems.  
*Polyporus betulinus* (Bull.) Fr., on the old birch tree, *nummularius* (Bull.) Quél., *picipes* Fr., *varius* Fr.

*Polystictus versicolor* (L.) Fr.  
*Poria vulgaris* Fr., *sensu* Rea.  
*Psathyra bifrons* B., *gossypina* (Bull.) Fr., *Typhae* Kalchbr. (see description at end of list).  
*Psathyrella atomata* Fr., *disseminata* (Pers.) Fr., *gracilis* Fr.  
*Psilocybe bullacea* (Bull.) Fr., *foeniseccii* (Pers.) Fr., *inquilina* (Fr.) Bres.  
*Russula violacea* Quél. under *Cornus*.  
*Solenia anomala* (Pers.) Fr.  
*Stereum hirsutum* (Willd.) Fr., *purpureum* (Pers.) Fr.  
*Tricholoma melaleucum* (Pers.) Fr., small specimens on the remains of *Cladium* in the carr.  
*Tubaria furfuracea* (Pers.) W. G. Sm.  
*Typhula candida* Fr., *erythropus* (Bolt.) Fr., *Grevillei* Fr., *gyrans* (Batsch) Fr., *phacorrhiza* (Reichb.) Fr.

#### HETEROBASIDIAE

*Coleosporium Rhinanthacearum* Lév., *Senecionis* Fr., *Sonchi* Lév., *Tussilaginis* Tul.  
*Doassansia Sagittariae* (West.) Fisch.  
*Exidia nucleata* (Schw.) Rea.  
*Melampsorella Symphyti* Bubák.  
*Phragmidium disciflorum* James.  
*Puccinia bromina* Erikss., *bullata* Wint., *Centaureae* DC., *Cirsii* Lasch., *Cnicolieracei* Pers., *coronata* Corda, *Glechomatis* DC., *holcina* Erikss., *Hypo-chaeridis* Oud., *Lolii* Niels., *Magnusiana* Körn., *Menthae* Pers., *obtegens* Tul., *Orchidearum-Phalaridis* Kleb., *persistens* Plowr., *Phragmitis* Körn., *Poarum* Niels., *pulverulenta* Grev., *Taraxaci* Plowr.  
*Sebacina fugacissima* Bourd. & Galz.  
*Tremella mesenterica* (Retz.) Fr.  
*Triphragmium Ulmariae* Wint.  
*Urocystis Anemones* (Pers.) Wint.  
*Uromyces Fabae* de Bary, *Junci* Tul., *Polygoni* Fuck., *Rumicis* Wint.  
*Ustilago longissima* (Sow.) Tul.

#### ASCOMYCETES

##### DISCOMYCETES

*Aleuria vesiculosa* (Bull.) Boud.  
*Ascobolus furfuraceus* Pers.  
*Ascophanus carneus* (Pers.) Boud., *ochraceus* (Cr.) Boud.  
*Belonidium vexatum* de Not.  
*Belonium excelsius* (Karst.) Boud., *filisporum* (Cke.) Sacc.  
*Calycella citrina* (Hedw.) Quél., *claroflava* (Grev.) Boud., *uliginosa* (Fr.) Boud.  
*Catinella olivacea* (Batsch.) Boud.  
*Cheilymenia dalmeniensis* (Cke.) Boud.  
*Ciboria amentacea* (Balb.) Fuck.  
*Ciliaria asperior* (Nyl.) Boud., *hirta* (Schum.) Rehm, *scutellata* (L.) Quél.  
*Coprobria granulata* (Bull.) Boud.  
*Coryne sarcoïdes* (Jacq.) Tul.  
*Cyathicula coronata* (Bull.) de Not.  
*Dasyobolus immersus* (Pers.) Sacc.  
*Dasyoscypha acutipila* (Karst.) Sacc., *bicolor* (Bull.) Fuck., *calyculaeformis* (Schum.) Rehm, *controversa* (Cke.) Rehm, *crucifera* (Phill.) Sacc., *crystallina* (Fuck.) Sacc., *patens* (Fr.) Sacc., *rosea* Rehm, *spiraæcola* (Karst.) Sacc., *virginea* (Batsch.) Fuck.  
*Dermatea Frangulae* (Fr.) Tul.  
*Encoelia furfuracea* (Roth.) Karst.  
*Erinella hapala* (B. & Br.) Sacc., *Nylanderia* Rehm.  
*Galactinia badia* (Pers.) Boud., *succosa* (Berk.) Sacc.

*Helotium amenti* Fuck., *cyathoideum* (Bull.) Karst., *eburneum* (Desm.) Gill.,  
*epiphyllum* (Pers.) Fr., *gramineum* Phill., *herbarum* (Pers.) Fr., *phyllogenum*  
 Rehm, *phyllophilum* (Desm.) Karst., *salicellum* (Hazl.) Fr., *scutula* (Pers.)  
 Karst., *tetra-ascosporum* Rea, *virgultorum* (Wallr.) Karst.  
*Heterosphaeria patella* (Tode.) Grev.  
*Hyalinia inflatula* (Karst.) Boud.  
*Hyaloscypha hyalina* (Pers.) Boud.  
*Lachnea hemisphaerica* (Wigg.) Gill.  
*Lachnella albotestacea* (Desm.) Quél., *canescens* (Phill.) Cke., *leucophaea* (Pers.)  
 Boud., *sulfurea* (Pers.) Quél.  
*Lasiobolus equinus* (Mull.) Karst.  
*Micropodia dumorum* (Desm.) Boud.  
*Mitrula sclerotipus* Boud. (see description at end of list).  
*Mollisia atrata* (Pers.) Karst., *benesuada* (Tul.) Phill., *cinerea* (Batsch) Karst.,  
*juncina* (Pers.) Rehm, *melatephra* (Lasch) Karst.  
*Niptera lacustris* Fr., *pulla* (Phill. & Keith) Boud.  
*Ombrophila clavus* (A. & S.) Cke., *imberbis* (Bull.) Boud., *verna* Boud.  
*Orbilia leucostigma* Fr., *xanthostigma* Fr.  
*Phacidium Calthae* Phill.  
*Phialea polaris* (Batsch) Quél.  
*Polydesmia pruinosa* (B. & Br.) Boud.  
*Pseudopeziza Trifolii* (Biv.-Bern.) Fuck.  
*Pyrenopeziza millegrana* Boud.  
*Pulvinula constellatio* (Cke.) Boud.  
*Sclerotinia Curreyana* (Berk.) Karst., *Duriaeana* (Tul.) Quél.  
*Sepultaria arenicola* (Lév.) Mass.  
*Tapesia evilesrens* (Karst.) Sacc., *fusca* (Pers.) Fuck., *retincola* (Rabenh.) Karst.,  
 common on dead haulms of *Phragmites*.  
*Trichopeziza carinata* Cke., & Mass., *Grevillei* (Berk.) Sacc.  
*Urceolella deparcula* (Karst.) Boud., *effugiens* (Desm.) Boud., *leucostoma* (Rehm)  
 Boud., *scrupulosa* (Karst.) Boud.

#### PYRENOMYCETES

*Anthostomella tonicum* (Lév.) Sacc.  
*Calonectria xantholeuca* (Kunze) Sacc.  
*Claviceps microcephala* (Wallr.) Tul.  
*Coleroa Chaetomium* (Kunze) Rabenh.  
*Didymosphaeria commanipula* (B. & Br.) Niessl.  
*Erysiphe Cichoracearum* DC., *communis* (Wallr.) Fr., *graminis* DC., *Martii* Lév.  
*Leptosphaeria doliolum* (Pers.) Ces. & de Not.  
*Lophiostoma caulinum* (Fr.) de Not., *microstomum* Niessl, *semilibatum* (Desm.)  
 Ces. & de Not.  
*Massaria eburnea* Tul.  
*Nectria cinnabarina* (Tode) Fr., *coccinea* (Pers.) Fr.  
*Ophiobolus herpotrichus* (Fr.) Sacc.  
*Phyllachora graminis* (Pers.) Fuck.  
*Pleospora herbarum* (Pers.) Rabenh.  
*Sphaerotheca pannosa* (Wallr.) Lév.  
*Trematosphaeria mastoidea* (Fr.) Rabenh.  
*Valsa lata* (Pers.) Nits.  
*Venturia Ruminis* (Desm.) Rabenh.

#### PHYCOMYCETES

*Cystopus candidus* (Pers.) Lév.  
*Peronospora alta* Fuck., *effusa* Rabenh., *nivea* Unger, *parasitica* (Pers.) Tul.,  
*Urticae* Casp.  
*Phycomyces nitens* Kuntze.

*Marasmius Menieri* Boud. in *Bull. Soc. mycol. Fr.* (1894), p. 61.

Pileus 2-6 mm. wide,  $120-250\mu$  thick, convex then *plane*, sometimes subconcave, rarely subumbonate, *circular* or *almost spatulate*, *puberulous*, even or subreticulate, not striate, *white* to *pale yellowish* or *brownish*: margin straight at first, often becoming slightly inflexed. Stem 2-10 mm. long,  $0.3-0.8$  mm. thick at the base,  $0.15$  mm. at the apex, *central* or *slightly excentric*, *generally more or less horizontal* and *pressed against the hymenium*, rarely vertical, *attenuate upwards from the abrupt swollen base*, *puberulous* below, *glabrous* above, *white* at the apex, *ferruginous* downwards, *dark brown* or *black* at the base. Hymenium *plane* or with a few shallow folds or wrinkles, *white* or *cream-coloured*. Flesh very thin, slightly gelatinous over the hymenium, *pallid*. Spores  $13-23 \times 4-5.5\mu$ , *white*, *smooth*, *fusiform* pip-shaped, *thin-walled*: clouded vacuolate. Basidia  $40-55 \times 9-11\mu$ , with 4, rarely 2, sterigmata,  $4-5\mu$  long. Cystidia absent from the hymenium. On decayed leaves of *Cladium Mariscus* and *Typha*, July-Oct.; common in the fens.

The upperside of the pileus is covered with a compact palisade of a single layer of clavate or ventricose cells,  $25-80 \times 12-30\mu$ , with slightly thickened, pale yellowish brown, even walls, often more or less encrusted, which give the colour to the pileus. There are also, in this layer, numerous ventricose pilocystidia,  $50-120 \times 6-18\mu$ , with thin, smooth, colourless walls and prolonged distally into a straight filiform appendage,  $1.5-2.5\mu$  wide. The caulocystidia are of two kinds, either like the pilocystidia and ventricose or subtriangular below with filiform apex, or like the palisade cells of the pileus but more irregular and narrower, cylindric to clavate and capitate, rarely encrusted,  $30-70 \times 5-20\mu$ , with darker brown walls, giving the colour to the stem.

Boudier states that there may be shallow gills: there were none in the Fen specimens, the folds and wrinkles of the hymenium corresponding with furrows on the pileus and not formed by a downgrowth of hyphae. When growing from a vertical surface, as from the leaf-bases of *Cladium*, the stem appears lateral because it is pressed tight against the hymenium.

*Pistillaria aculeata* Pat. *Tab. Anal.* No. 58.

R. 1-2 mm. high,  $40-90\mu$  thick, with a distinct, *glabrous* stem,  $0.2-0.4$  mm. long, *minute*, *filiform*, simple, not swollen at the base, *attenuate at the apex*, *white*. Hymenium loose, generally leaving a sterile apex, rarely continuous over the apex. Spores  $4-6 \times 2-3\mu$ , *white*, *smooth*, *ellipsoid*, slightly flattened on the inside, with thin walls and clouded contents. Basidia  $8-16 \times 3.5-5\mu$ , subclavate with 4, rarely 2, sterigmata,  $3-6\mu$  long, not forming a compact layer. Cystidia none. Hyphae  $1-2.5\mu$ , with clamps. Densely gregarious on dead leaf-bases of *Cladium Mariscus*, July-Nov.; common.

*Pistillaria graminicola* differs in the hairy stem and larger spores. *P. Queletii* Pat. differs in being sessile and having cystidia. *P. acuminata* Fuck. differs in the thicker, squat receptacle and much smaller spores. *P. mucedinacea* Boud. has narrower, subcylindric spores, according to Bourdot and Galzin (*Hym. Fr.* p. 137), and is lignicolous, though in other respects exceedingly similar. As noted by Bourdot and Galzin (*loc. cit.* p. 140), the receptacle may or may not have a sterile apex according to its state of development.

*Pistillaria aculina* (Quél.) Pat.; Quél. in *Ass. Fr.* (1880), p. 10.

R. 3-10 mm. high,  $0.1-0.3$  mm. thick, *small*, *acicular*, *attenuate to the filiform apex*, rarely subcylindric with obtuse abrupt apex, *sessile* or indistinctly stipitate, simple, *white*; base slightly dilated, often brownish. Hymenium compact, continuous from the base to some distance short of the apex which projects as a sterile point, rarely continuous over the apex, sometimes lacking at the extreme base. Spores  $9-13 \times 6-7\mu$ , *white*, *smooth*, *ellipsoid*, slightly flattened on the inside, with thin walls and

clouded contents. Basidia  $20-28 \times 7-9 \mu$ , clavate, with 2 sterigmata,  $4-5 \mu$  long. Cystidia  $25-40 \times 5-8 \mu$ , frequent, varying from sterile basidia, narrowed at the apex, to subventricose, elongate cells with bluntly tapered apex. Hyphae  $1.5-3 \mu$ , with clamps. Gregarious on dead haulms of grasses, sedges and rushes, Oct.-Nov.; common in the fens.

This species differs from *P. aculeata* in the larger, sessile receptacles, the larger spores, the 2-spored basidia and the presence of cystidia. The numerous subspecies described by Bourdot and Galzin (*Hym. Fr.*, pp. 138, 139) may also be found on the Fen.

***Pluteus hispidulus* Fr.; Konr. & Maubl. *Ic. Select. Fung.* t. 25, f. 1.**

Not uncommonly, scattered on the ground in the carr, are to be found the fruit-bodies of a *Pluteus* which Rea would refer to *P. hispidulus* Fr., *sensu* Konrad and Maublanc, with whose description and figure it well agrees. The pileus is darker and much more villous, however, than one would imagine from Fries's description and it is always terrestrial (I have found it on Chippenham Fen also, and in Bucks). On the other hand it agrees exactly with *P. exiguis* Pat. (*Tab. Anal.* No. 425) apart from the spores which Patouillard gives as  $6-7 \times 3 \mu$ . *P. murinus* Bres. is close but has much larger fruit-bodies with paler and less villous pilei. *P. plautus* differs in the dark villous stem and *P. cinereus* in the white furfuraceous stem. I append a description of the fungus from Wicken Fen by which it may be recognised and finally determined.

Pil. 1-2 cm., convex becoming plane, finally often depressed in the centre, *at first wholly mouse-grey, fuliginous fuscous or blackish brown and velvety-villous*, with the disc darker and often umber-black, *developing a ruddy tinge towards the margin as the pileus expands and the villosity breaking up into minute erect umber-black scurfy squamules*,  $0.3-0.5$  mm. high, except at the disc which remains evenly villous: margin straight, becoming slightly sulcate over the gills, not striate. Stem  $3-3.5 \times 0.15-0.2$  cm., cylindric, hollow, brittle, *shining watery white to silvery grey, silky fibrillose with a few darker, fuscous fibrils especially towards the abrupt slightly swollen white villous base*. Gills free or just adnexed, ventricose, crowded,  $3-3.5$  mm. wide, 1-2 ranks, white then pink. Flesh thin, watery white; smell none. Spores pink subglobose, smooth,  $5-7 \times 5-6 \mu$ . Basidia  $20-30 \times 7-9 \mu$ , with 2-4 sterigmata. Cystidia only on the gill-edge, not forming a sterile edge, vesiculose, clavate or ventricose, often prolonged into a short appendage, not hooked, thin-walled, colourless,  $35-60 \times 9-13 \mu$ . On wet earth rich in humus. June-Sept.; frequent on the Fen.

The hyphae forming the villosity of the pileus are in a pile perpendicular to the surface and composed of several cells,  $40-150 \times 8-30 \mu$  with dark brown sap, the terminal cell varying from clavate to ventricose.

***Psathyra Typhae* Kalchbr. *Gomb.* p. 206, t. 1, fig. 1, and *Psathyra Typhae* var. *Iridis* Boud. in *Bull. Soc. mycol. Fr.* XIII (1897), 13, t. 1, Fig. 3.**

Pileus  $1-1.5$  cm., convex then flattened, sometimes depressed in the centre, *disc sometimes vaguely reticulate*, otherwise smooth and even, *striate, hygrophanous, watery fuscous fawn to watery cinnamon, darker at the disc when moist, drying pallid fuscous tan and minutely atomate*; margin straight. Veil thin, fugacious, as a few brownish fibrils round the margin of the pileus and fibrils on the stem, sometimes forming a faint arachnoid ring on the stem. Stem  $2-3$  cm.  $\times 1-1.5$  mm., *brittle, cylindric, somewhat white fibrillose in the lower half, apex slightly striate, pallid with a faint tinge of brown; base abrupt, swollen, 3-4 mm. wide, white villous*. Gills rounded adnexed, separating free sub-distant,  $2-2.5$  mm. wide, *pallid white then fawn*. Flesh very thin, concolorous, fragile. Spores  $10-13 \times 6-7.5 \mu$ , fuscous fawn in the mass, yellowish fuscous under the microscope, smooth, elliptic more or less deformed on one side, rarely sub-

triangular, eguttate. Basidia  $27-40 \times 10-14\mu$  with 4 sterigmata. Cystidia only on gill-edge forming a sterile edge, clavate, cylindric or more or less ventricose, often curved or flexuous, thin-walled, colourless,  $20-50 \times 8-16\mu$ . On dead stems and leaves of *Phragmites*, *Carex*, *Scirpus*, in wet places, often just above the water-level on leaf-bases attached to the dead standing stems. July-Sept. Fens, Cambridgeshire.

***Mitrula sclerotipus*** Boud. in *Bull. Soc. bot. Fr.* (1877), 309, t. iv, Fig. V; *Icon. Mycol.* III, pl. 428, IV, 245; *Trans. Brit. mycol. Soc.* III, 378.

Very small, 1.5-2 cm. long, yellowish ferruginous, club oblong, shorter than the stem. Club elongate, club-shaped, generally narrower at the base, separated from the stem by a distinct groove, solid, flesh white or concolourous when moist. Stem stuffed, simple, occasionally bifurcate or trifurcate, springing from a well developed sclerotium. Paraphyses shorter than the asci, hyaline, granular inside. Asci fusiform,  $45-50 \times 5-7\mu$ . Spores  $10-13 \times 3-3.5\mu$ , filled with multigranular protoplasm. On the ground in marshy woods. June. Common in the Fen.

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NOTES ON THE OCCURRENCE OF *PYRENOPHORA AVENAE* ITO, IN SCOTLAND

By R. W. G. DENNIS, PH.D.

(With 9 Text-figures)

IN some notes<sup>(1)</sup> recently compiled on the *Helminthosporium* disease of oats in Scotland it was pointed out that although the perfect stage of the fungus had been reported by Rathschlag<sup>(4)</sup> in Germany, and by Ito<sup>(3)</sup> in Japan, it had not been found in this country. Attention was also drawn to the fact that discrepancies exist between the descriptions furnished by these authors, and it was suggested that the findings of Ito might be inapplicable to European conditions.

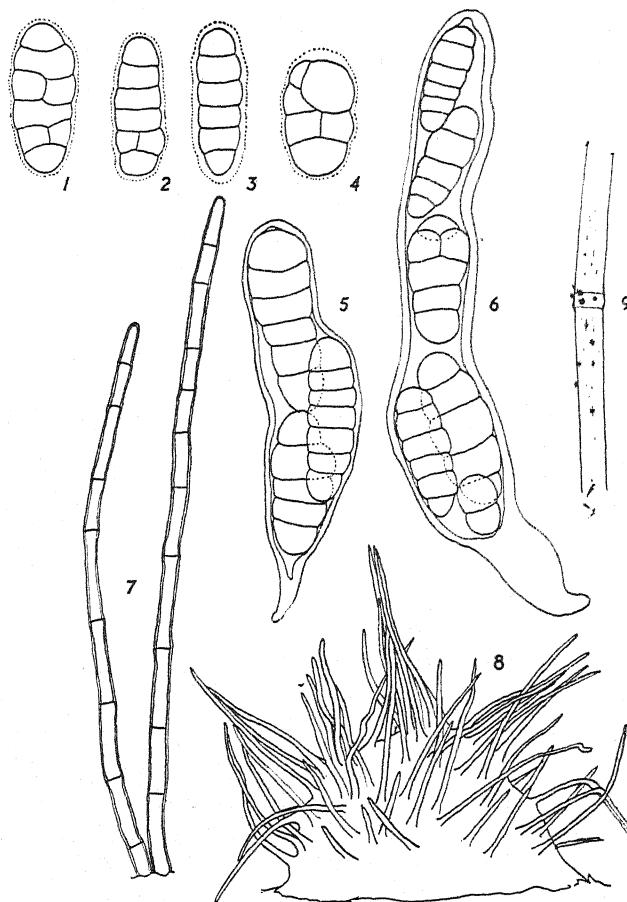
Since the above paper was written perithecia associated with *Helminthosporium Avenae* have been discovered in Scotland. Unfortunately, as in the closely related *Pyrenophora teres* described by Drechsler<sup>(2)</sup>, the majority of the asci have remained immature. Sufficient material however, is available to indicate that the fructifications correspond closely with the diagnosis furnished by Ito, and differ widely from the structures obtained under cultural conditions by Rathschlag.

Perithecia were first observed on January 16th, 1934, on stubble of King Oat sown out with grass at Auchincruive, Ayrshire. Specimens were scarce at this period, a collection of 283 stems showed only 8, or 2.9 per cent., with fructifications, and of these only one contained mature ascospores. Single spore cultures were at once made from these, and exhibited the peculiar tufted development of aerial mycelium characteristic of *H. Avenae*. *Helminthosporium* spores were being produced freely on these cultures by February 14th.

As the season advanced perithecial rudiments became more frequent on the stubble, but the proportion of fructifications containing mature asci has remained extremely low, even as late as the month of May.

Perithecia originate below the host epidermis but soon become erumpent, and visible to the naked eye as black granules about 0.5 mm. across, adhering to the surface of the straw (Fig. 9). They may develop at any point, but when only a few occur there is a distinct tendency for them to be clustered at the nodes. Perithecia of *Pyrenophora* may be readily distinguished in the field from all other fructifications found on the stubble, with the exception of *Vermicularia*, by their thick coating of setae, which are clearly discernible when the specimen is held to the light. They are semi-globose when young

(Fig. 8) and about  $600 \times 700\mu$  in diameter, but may show indications of an ill-defined ostiolar beak as they approach maturity. The fructifications are covered with stiff, dark brown setae tapering



Figs. 1-4. Ascospores of *Pyrenophora Avenae*.  $\times 250$ .

Figs. 5, 6. Asc.  $\times 250$ .

Fig. 7. Setae from perithecioid.  $\times 250$ .

Fig. 8. Immature perithecioid from oat stubble.  $\times 60$ .

Fig. 9. Oat stubble bearing perithecia of *P. Avenae*. Nat. size.

slightly to their rounded ends. Interspersed sometimes with these are dead conidiophores, readily distinguished by their knee-shaped bends. The length of the setae is very variable but commonly as much as  $280\mu$ , their thickness being  $7-9\mu$ , greatest at the cross-walls (Fig. 7). Similar bodies, but containing no ascospores, have been obtained in old

pure cultures of *H. Avenae* on sterilised straw. In agar cultures only sclerotia devoid of setae have been observed.

The asci apparently mature very slowly, and in succession, so that a single fructification may yield all stages from a body  $120\mu$  long with unorganised granular contents, to an apparently mature ascus  $280 \times 50\mu$ , containing ripe ascospores. They are hyaline, slightly curved structures, with short stipes and rounded apices. The wall is thickened towards the apex and exhibits a well-marked apical pore (Figs. 5 and 6). In the material available the asci contain from 3 to 6, usually 6, yellowish brown ascospores, each exhibiting 3-6 transverse septa, usually 5. One or more of the component cells is usually divided into two by a longitudinal wall, but spores have not been obtained so markedly muriform as those figured by Rathschlag (4). The spores are distinctly constricted at the transverse septa and are surrounded by a hyaline mucilaginous investment, clearly seen when they are mounted in water (Figs. 1-4). Spore dimensions vary according to the number in the ascus but the most normal specimens lie between  $49-63 \times 21-25\mu$ .

The correspondence of the Scotch specimens with Ito's diagnosis of *Pyrenophora Avenae* is brought out in the following table:

Ito	Scotch perithecia	Rathschlag
Perithecia setose	Perithecia setose	No setae
Perithecia 450-800 $\times 350-700\mu$	Perithecia up to 800 $\mu$	Perithecia 118-140 $\mu$
Asci 250-350 $\times$ 35-45 $\mu$	Asci up to 280 $\times$ 50 $\mu$	Asci 192 $\times$ 29 $\mu$
No. of ascospores 2-8	No. of ascospores 3-6	No. of ascospores 8
Spores 50.75 $\times$ 17.5-30 $\mu$	Spores 49-63 $\times$ 21-25 $\mu$	Spores 33 $\times$ 14 $\mu$
No. of transverse walls 3-6	Transverse walls 3-6	Transverse walls 5-8
Longitudinal septa few	Longitudinal septa few	Longitudinal septa many

The genetic connection of Rathschlag's perithecia with his species of *Helminthosporium* cannot be denied. They were obtained in pure culture and the ascospores were found capable of reproducing the leaf stripe disease in oats. Nor does Rathschlag's description of his strain of *H. Avenae* indicate any divergence from the common type. It appears probable, therefore, that the peculiar features of his *Pleospora Avenae* are best ascribed to its development under artificial and presumably somewhat unfavourable conditions.

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## ON VARIATION IN *THAMNIDIUM ELEGANS* LINK, INDUCED BY THE ACTION OF HIGH TEMPERATURES

By B. BARNES

(*Head, Department of Biology, Chelsea Polytechnic,  
London, S.W. 3*)

(With Plates XIII and XIV and 10 Text-figures)

IT has been shown that variant forms of *Eurotium herbariorum* (Wigg.) Link<sup>(2)</sup>, and of *Botrytis cinerea* Pers.<sup>(3)</sup> can be obtained by heating conidia of these fungi, and then planting the spores on ordinary media. It has also been shown that some of the variant forms persist in culture without any further use of high temperatures, and that there is some relation between the degree of initial change and the degree of constancy of the new forms. It seemed desirable to continue the work with a third fungus, and for this purpose *Thamnidium elegans* was selected. A strain of this species had been in my possession since 1922, and was known to be constant in its behaviour when grown on potato agar. It was known, too, that *T. elegans* was not a common member of the weed flora of the laboratory in the Department of Botany, Birkbeck College (University of London), where the work was done. Since 1922 it had occurred only once in numerous cultures started from rat dung collected in the building, and never developed in cultures inoculated with pigeon dung taken from the roofs and window-sills near the laboratory. Although, during the past twelve years, many plates of various media have been purposely contaminated with dust, *T. elegans* appeared in these cultures only at times when it was known that spores had been recently liberated into the room. If, therefore, the normal form of the species is infrequent in the laboratory, abnormal forms should be still more uncommon. These considerations indicated that there was little danger of experimental cultures being infected with *Thamnidium* from without. Therefore, as a well-tested strain was available, and as the striking morphology of the species offered interesting possibilities of change, experiments were begun in the summer of 1929. Variants were soon obtained, but the preparation of an account of the work has been purposely delayed, in order that the constancy of the variants in culture might be tested over a long period. By the end of 1932, it was clear that reversion to the normal form was far advanced in two variants, while a third and more extreme variant appeared to have settled down into a permanent form distinct from normal.

## CULTURAL DETAILS

Potato agar\* has been used as the substratum for all the cultures made in this investigation. The dishes have been incubated for at least three days after pouring, and examined before inoculation to ensure that they were clean at that time; the plates were not opened for this examination, which was made through the lids. The cultures have been kept in the open laboratory, and no attempts have been made to regulate the supply of heat and light. Control cultures, cultures started from heated spores, and routine cultures of the normal and variant forms have been mixed in stacks. Frequent changes in the positions of the stacks, and of the Petri dishes in the stacks, have cancelled out any slight environmental differences. Special precautions have been taken to prevent the entry of mites, by keeping the stacks of cultures on supports surrounded by water(4), by handling the dishes as little as possible, and by placing them when under inspection on glass surfaces freshly cleaned with methylated spirit. Petri dishes taken from the stacks for observation have been wiped with methylated spirit as a preliminary to further handling, so reducing the risk of contamination from dust. Inoculations have been made with cool sterile instruments in a quiet room, the dishes being manipulated on clean sheets of glass, wiped between each inoculation with spirit. These precautions have made it possible to keep the cultures in a satisfactory condition of purity. This communication is based on the examination of over one thousand six hundred cultures, all of which have been kept free from the ordinary "weeds" known to occur in the laboratory. As the usual intruders have been successfully excluded from the cultures, the appearance of the variants cannot reasonably be ascribed to infection from without.

## EXPERIMENTS WITH HEATED SPORES

In July 1929, single-spore cultures were prepared by a dilution method. Weak suspensions of spores taken from a clean culture of the stock strain of *T. elegans* were made in distilled water, spilled on potato agar, and spread by suitably inclining the dish. After about an hour, the surface of the agar was examined through the lid of the dish, and the positions of well-isolated spores were marked. As soon as growth was visible, ten sporelings were picked out and transferred singly to fresh dishes. The new cultures were examined at intervals of a few hours, and in this way it was established that all the growth present in each dish had arisen from the single sporeling used to start the culture. In due course, mature spores from one of these cultures

\* Potatoes, 250 gm.: shred, steam for 1 hour, decant off extract and filter, make up to 1 litre, add 20 per cent. agar, autoclave at 30 lb. pressure for 20 min., and pour hot.

were suspended in distilled water. After thorough agitation, the suspension was poured, in small amounts, into a number of tubes. From one of these, after further shaking, 0.5 c.c. of the suspension was transferred to a dry tube, which was then shaken vigorously in a water bath at a given temperature for a given time. As soon as the time had expired, the suspension was at once spilled on the surface of potato agar in a dish, and spread by inclining the dish. Further lots of spores were similarly treated, each lot being taken from a fresh sample of suspension. Control cultures were prepared, at the same time, from unheated lots of suspension. In these operations, as in all the experiments with heated spores, the distilled water, media and glass ware were carefully sterilised before use.

The cultures were examined at intervals of a few hours during the

Table I. *Experiments with heated spores of Thamnidium elegans, 25. vii. 29*

Temp. °C.	Time min.	No. of cultures	Notes
45	2	2	Growth normal, 12-20 colonies in each
50	2	2	One culture normal; one with slight retardation in early growth, then normal
55	2	2	One culture normal. The other (culture 55.2) contained 14 normal colonies and two light-coloured colonies of weak growth; these yielded variants
60	2	2	No growth
65	2	2	No growth
70	2	1	Eight normal colonies and one light-coloured variant with large heads of sporangiola. This yielded a variant
75	2	1	No growth
80-100	2	5	No growth

Ten controls, all normal, each with 15-20 colonies.

Table II. *Experiments with heated spores of Thamnidium elegans, 1. viii. 29*

Temp. °C.	Time min.	No. of cultures	Notes
45	1	2	Growth normal
45	2	2	„
45	3	2	„
50	1	2	„
50	2	2	„
60	1	2	Early growth slightly retarded; normal later Retardation in early growth. Two colonies, light in colour, and with large heads of sporangiola; not taken into culture
60	2	2	No growth in one. In the other, a single colony, light in colour, and of slightly retarded growth; a subnormal form, not taken into culture
60	3	2	No growth in one. In the other, a weak, sterile mycelium which soon died
70-100	1-3	24	No growth

Ten controls, all normal, with 17-22 colonies.

first two days after preparation, special attention being paid to the rate at which the spores germinated, and to the appearance of the young colonies. The results of the first two sets of experiments are given in Tables I and II.

From the cultures listed in Table I, two well-marked variants, and a third of less obvious character, were isolated. From these isolations, long series of cultures were started. Attempts were made to propagate the weak sterile mycelium noted in Table II. This mycelium was certainly phycomycetous, and presumably belonged to *Thamnidium*. It reached a diameter of 0.8 cm. in the original culture, then ceased to grow, and died out. The growth was weak and deformed, remaining quite sterile. Six hyphal transfers were made to fresh potato agar, but they all failed to establish themselves. This weak form may be compared with the variants of reduced vitality found in *Botrytis cinerea* (3), p. 840.

During 1930 and 1931, additional experiments were made with heated spores, using the methods already described; 314 cultures were started from heated spores, and 102 control cultures, from unheated spores, accompanied them. The results of these experiments showed general agreement with those given in Tables I and II. Cultures from unheated spores never produced any abnormal colonies; cultures from heated spores gave variants in about the same proportions, and in the same erratic fashion as the cultures of the earlier experiments. None of these variants was noticeably distinct from variants already in culture and none was taken into prolonged culture. Spores exposed to temperatures below 50° C. never gave a variant. After treatment at 50° C. there were usually signs of retardation of early growth, though the mature colonies appeared to be normal. Spores treated between 55 and 70° C. gave some colonies apparently normal, and others with large or with small heads of sporangiola, and light in colour. With increasing temperature there was decrease in the number of germinations; growth was never obtained from spores which had been heated to temperatures exceeding 70° C.

#### ISOLATION OF THE VARIANTS OBTAINED IN 1929

Spores taken from the abnormal colonies noted in Table I were suspended in quantities of 0.5 c.c. distilled water, and spread on potato agar in the manner already described: the suspensions were not heated. Control cultures from normal spores were prepared at the same time. Next day, examination showed that the cultures started from the abnormal colonies in the original experimental dishes contained sporelings readily distinguishable from normal sporelings by their small size and irregular branching; at this time it was easy to see that the sporelings had developed from single spores. Small,

irregular sporelings were of general occurrence in the progeny of the abnormal colonies; none developed from spores taken from normal colonies. The characteristic peculiarities of the variants were shown equally by sporelings growing close together, and sporelings well separated on the medium; therefore they were not due merely to the effects of competition. On the second day after the preparation of these cultures, some of the more irregular of the abnormal sporelings were transferred separately to fresh dishes. From these transfers, three distinct variants were ultimately isolated: they will be referred to as the large-headed variant, the dwarf variant and the subnormal variant.

Series of cultures, made up of successive sets—a set being the lot of cultures made up on a given date—have been grown of the variants and of the normal form. The cultures, for the most part, have been started by transfers of spores with a cool platinum wire; only occasionally have single spore isolations been made. The mass transfers of spores eliminate the possibility that the maintenance of the variants in culture has been due to the continued selection of specially abnormal material. Sets of cultures of all the variants have not always been made on the same day, but normal cultures have always been started whenever variants have been transferred; consequently the number of sets of normal cultures shown in Table III is in excess of the number of sets of any one of the variants.

Table III. *Summary of cultures of Thamnidium elegans, normal and variant, on which this account is based*

Type	Series	Number of sets in series	Number of cultures in series	Period during which the series was under observation
Normal form	C	73	234*	August 1929–December 1932
Dwarf	DA	68	187	August 1929–December 1932
Dwarf	DF	25	71	August 1929–July 1930
Dwarf	DH	21	38	August 1929–May 1930
Subnormal	DJ	10	17	August 1929–March 1930
Subnormal	DK	58	136	August 1929–December 1932
Large-headed	M	62	170	October 1929–December 1932
Large-headed	P	67	172	August 1929–December 1932
Large-headed	Z	32	79	August 1929–October 1930

\* This number does not include the control cultures used for comparison with cultures started from heated spores.

#### THAMNIDIUM ELEGANS AND ITS VARIANTS

(a) *Normal Thamnidium elegans*. (Pl. XIII, figs. 2 and 5; Pl. XIV, figs. 9 and 12)

In the normal form of *T. elegans*, fertile axes arise in large numbers from the prostrate vegetative mycelium, and commonly terminate in large sporangia, which, like those of *Mucor*, contain each a columella

and many spores. In addition, dichotomising branch systems develop on the sporangiophores in superposed lateral tufts, and bear small sporangia—the sporangiola—at the ends of their ultimate ramifications. A sporangiolum does not possess a columella, and contains but few spores; these differ in no known way from the spores formed in the large sporangia. A brown pigment is present in the walls of the spores, other parts of the fungus being colourless, or but slightly coloured.

*Development in culture of normal T. elegans.* Spores of the stock strain germinate in a few hours after they are placed on potato agar; twelve hours after planting, the germ tubes have a length of four to six spore diameters, and have begun to branch. A colony a day old is easily visible to the naked eye (Text-fig. 1 a). Young colonies are rather loose in growth, and, for the first two or three days, main hyphae running radially outwards from the position occupied by the spore are readily distinguished; owing to swelling, the spore is seldom recognisable as such, a few hours after germination has occurred. The main hyphae spread radially and evenly on the medium (Text-fig. 2 a). Lateral hyphae develop from them at fairly regular intervals, and, as the main hyphae diverge, some of the laterals elongate rapidly in the free space and begin to function as main hyphae. Some hyphae penetrate the medium, but in early stages of growth they are few. Aerial branches seldom become strong until the colony is about two days old, and has formed a fairly dense edge, lying on the medium; they develop first in a central tuft of small heads of sporangiola on short stalks, large *Mucor*-like sporangia not yet being abundant. During the next two or three days, long sporangiophores ending in large sporangia arise in large numbers from the centre of the colony, the tuft becoming a conspicuous feature of the culture. Lateral tufts of sporangiola form abundantly on the sporangiophores, and, beneath this tall growth, which if space permits may attain a height of several centimetres, small terminal heads of sporangiola on short hyphae continue to form in limited numbers. By the fifth or sixth day, although sporangiophores are developing freely, they no longer make dense masses, and the aspect of the culture is now largely determined by the tufts of sporangiola, which increase in number and size. As the growing edge of the colony approaches the edge of the medium, the hyphae composing it begin to branch in an irregular manner, long sporangiophores with lateral tufts of sporangiola cease to grow abundantly, and short hyphae ending in terminal heads of sporangiola again become prominent. Throughout the life of the colony, large sporangia on short sporangiophores without lateral sporangiolic tufts develop in small numbers, but they are never abundant.

The lateral groups of sporangiola are dense, as the dichotomous branch systems composing them fork frequently, and consist of relatively short members. Large heads may exceed 0.5 mm. in dia-

meter, and some exceed 1 mm. in diameter. The average diameter of five hundred heads measured at random was 0.3 mm.

The normal form of *T. elegans* covers a surface of potato agar, 9 cm. in diameter, in from eight to nine days. By this time the centre of the colony is brownish (Ridgway, 17", *i* to *k*), but the edge, where unripe sporangiola abound, is white. The whole culture is uniformly brown by the fourteenth or the fifteenth day.

More than three hundred cultures of the normal form have been closely examined at all stages of their growth. None of these cultures showed any noteworthy divergence from the general behaviour just described, and in no culture was anything resembling the variants seen. The cultures confirmed the impression gained between 1922 and 1929, that the stock form of *T. elegans* is very steady in behaviour in ordinary culture.

From time to time, sets of cultures of the normal form have been made from parent cultures of diverse ages. Spores have been taken from cultures only three days old, and from old, dry cultures ninety days old; between these extremes, many intermediate ages were tested. Evidence was not obtained that, within these limits, the age of the spores had any influence on the characters of the colonies they yielded. Cultures started from hyphae grew like cultures started from spores.

(b) *Variant forms of Thamnidium elegans*

When the three variants were first isolated in 1929, they differed from the normal form in rate of growth, colour, and in the average dimensions of the heads of sporangiola. These characters were sufficiently obvious to allow of the examination of the cultures without opening the dishes, a very necessary condition when contamination had to be avoided.

(1) *The large-headed variant (Table III, Series M, P, Z).* (Pl. XIII, figs. 1, 4, 6 and Pl. XIV, figs. 8, 11.)

The large-headed variant was isolated from a colony of loose growth and light colour, obtained from a lot of spores heated to 70° C. for two minutes (Table I). Three isolations were made by the dilution method, when the original colony was twenty, twenty-five and sixty days old respectively. All the sporelings from these isolations were distinct in character from normal sporelings, and, as all appeared to be of the same kind, one only was taken from each isolation for further investigation: the three sporelings selected were the starting points of Series M, P and Z (Table III).

The variant came out clean from the first, and has behaved in the same way in the three series; it is the most extreme of the variants described in this communication, and, up to the time of writing,

has shown no marked indications of reversion to the normal condition.

*Development in culture of the large-headed variant.* Spores of the large-headed variant germinate fairly rapidly; germ tubes are present in twelve to eighteen hours after planting. Young colonies about a day old (Text-fig. 1 c) have a weak, stunted appearance, and consist of little more than a few main hyphae. As the colony develops, it becomes surrounded by a spreading prostrate edge, but in this, the main hyphae (Text-fig. 2 b) branch less freely than those of normal *T. elegans*, and do not give the regular pattern characteristic of the ordinary strain.

Aerial hyphae begin to form in large numbers when the cultures are three or four days old. The first to form may remain sterile, but most ultimately bear heads of sporangiola. The aerial hyphae of the large-headed variant react much more strongly to light than do the aerial hyphae of the stock strain; in one-sided illumination, positive phototropic response may be so strong that the hyphae lie nearly horizontally. There are rarely straight or evenly curved, for they are commonly formed like a loose and much elongated corkscrew (Text-fig. 6 b).

A culture of the large-headed variant four days old possesses a central tuft of sporangiolic heads, with some terminal sporangia. As growth proceeds, this tuft spreads outwards, but, as in normal cultures, seldom extends to the margin of the medium. Terminal sporangia form in fair numbers, some on the ends of long sporangiophores, some on short sporangiophores without lateral tufts. Small heads of sporangiola are also produced, but they are not abundant. When the cultures are eight to ten days old, the central area is light brownish (Ridgway, xl, 21", f) and this colour spreads to the periphery as the sporangiola mature. It is, however, soon hidden by a rich development of sterile hyphae, hiding the mature sporangiola and often rendering the culture snow-white. The white condition is reached in from fourteen to twenty-one days, so that old cultures of the variant differ noticeably from normal cultures of the same age (Pl. XIII, figs. 4 and 5).

The sporangiolic tufts of the large-headed variant are considerably larger than normal heads; they frequently exceed 1 mm. in diameter. The average diameter of five hundred heads was 0.54 mm.

The early cultures of the variant grew about half as fast as did normal cultures: the growth rate has since increased, and appears to have settled down at about three-quarters the normal value.

(2) *The dwarf variant* (Pl. XIII, figs. 3 and 7; Pl. XIV, figs. 10 and 13).

The dwarf variant was obtained from one of the light-coloured colonies in Culture 55.2, Table I. Preliminary transfers from this

colony gave sporelings of stunted and irregular appearance (Text-fig. 1 b); one of these was transferred to a fresh dish. The resulting colony developed in a peculiar manner. Growth was slow and weak, the colony being only 1.4 cm. in diameter when the corresponding control colonies had covered a surface 9 cm. in diameter. At that time, nine days after transfer, the mycelium bore a few small, whitish heads of sporangiola, scattered irregularly over the surface on short stalks; long sporangiophores and large sporangia were absent. After fourteen days, the colony was 4.5 cm. in diameter. Heads of sporangiola were still few, and large sporangia were not present. On the fourteenth day, a central tuft of long aerial hyphae began to form; they were all sterile, and, like those of the large-headed variant, they reacted strongly to light, and were loosely spiral in shape. Next day weak signs of sectoring were noted, and, when the colony was three weeks old, it consisted of two distinct areas, one bearing aborted sporangiophores, and no good fructifications, the other thinly covered by small heads of sporangiola on short erect hyphae.

Isolations were made from both areas. Spores from the sporangiola gave clean cultures of the dwarf variant (Series DA, Table III). Hyphal transfers from the edge of the other region also yielded cultures of the same type (Series DH, Table III).

Subsequently, further isolations were made from the original variant colony in Culture 55.2, Table I. These yielded clean cultures of the dwarf variant (Series DF, Table III). Series DF and DH were continued for about a year, and then discontinued, as the cultures composing these series agreed in all respects with the cultures of Series DA.

The peculiar behaviour of the colony which sectored was not repeated in any of the cultures derived from it, so that the initial instability indicated by the sectoring soon disappeared from the strain. Instability in colonies grown from heated spores, or in the offspring of such colonies, was noted in *Eurotium herbariorum* (2), and in *Botrytis cinerea* (3); in the latter it persisted through a number of cultures.

*Development in culture of the dwarf variant.* In the earlier cultures of the dwarf variant, the spores germinated more slowly than normal spores, and, usually, germ tubes were not visible twelve hours after the spores were sown. Small colonies developed within twenty-four hours; these colonies had an average diameter one-quarter that of normal colonies of the same age, and they had a characteristic aspect owing to the development of many short lateral branches. The colonies continued to grow about half as fast as the controls. The growth was low and thin, and, in the spreading edge of the mycelium, the main hyphae pursued a curved course, and bore their lateral branches unevenly, showing but a faint suggestion of the even pattern usual in normal mycelia of *T. elegans*. Many hyphae grew into the medium.

At least fourteen days were required for the colony to cover a surface 9 cm. in diameter. Mature colonies differed greatly in appearance from mature controls. Dense tufted growth was absent, even from the centres of the colonies, large sporangia on long sporangiophores were scantily present, and the sporangiolic heads, at the ends of remarkably short stalks, were thinly scattered about the culture. The heads of sporangiola were small; it was rare to observe one which exceeded 0.5 mm. in diameter. The average diameter of five hundred heads was 0.16 mm. Old cultures were light brown (Ridgway, XL, 17", b to -).

As in the large-headed variant, the growth rate increased during the first few months of culture, but did not attain normality. The morphological peculiarities were retained almost unchanged for over a year, though, as time went on, there was a gradual increase in general strength, which, unfortunately, cannot be expressed in any definite manner. By the end of 1931, when the dwarf variant had been in culture for over two years, and had passed through 55 transfers, it was still distinct from the normal strain; in particular, the production of stunted sporelings was a feature of the variant. During 1932, reversion to normal became more pronounced, and, by the end of that year, mature cultures of Series DA were not greatly different from normal cultures, though a slight weakness in growth was still demonstrable.

### (3) *The subnormal variant.*

The subnormal variant was isolated from the second light-coloured colony in Culture 55.2, Table I. The first isolations gave colonies clearly distinct from normal colonies; from these two series (Series DJ and DK, Table III) were started. Series DJ was discontinued when it was obvious that the cultures were alike in Series DJ and DK.

The subnormal variant did not differ much from normal except in one respect. In the early cultures of Series DJ and DK, rich crops of large sporangia, carried on short sporangiophores without lateral tufts of sporangiola, developed in the growing edges of the colonies. It was suspected that the cultures were contaminated by a small species of *Mucor*, but single spores taken from the sporangia reproduced the variant, and removed all doubts. In strength of growth, sporeling characters, manner of branching of the hyphae in the spreading edge of a colony, in colour, and in the extent to which small heads of sporangiola developed, the subnormal variant was intermediate between the normal and the dwarf forms.

It was evident by October 1929, when this variant had passed through eight transfers, that the production of many sporangia on short stalks was falling off, but the cultures were still somewhat thinner and weaker in general growth than normal cultures. By the

summer of 1931, when thirty-seven transfers had been made, it was hardly possible to distinguish cultures of the subnormal variant from ordinary cultures, but, as will be shown presently (p. 310), it is possible that complete reversion had not occurred, for the variant retained a tendency to develop more spores in the sporangiola than did the normal *T. elegans*.

Table IV summarises the notes made on a set of cultures three days old, started by single colony transfers in May 1931, nearly two years after the variants were induced. The information gives some measure of the differences existing between the four forms at that time.

Table IV. *Thamnidium elegans*, *normal and variant*  
(*three cultures of each type*)

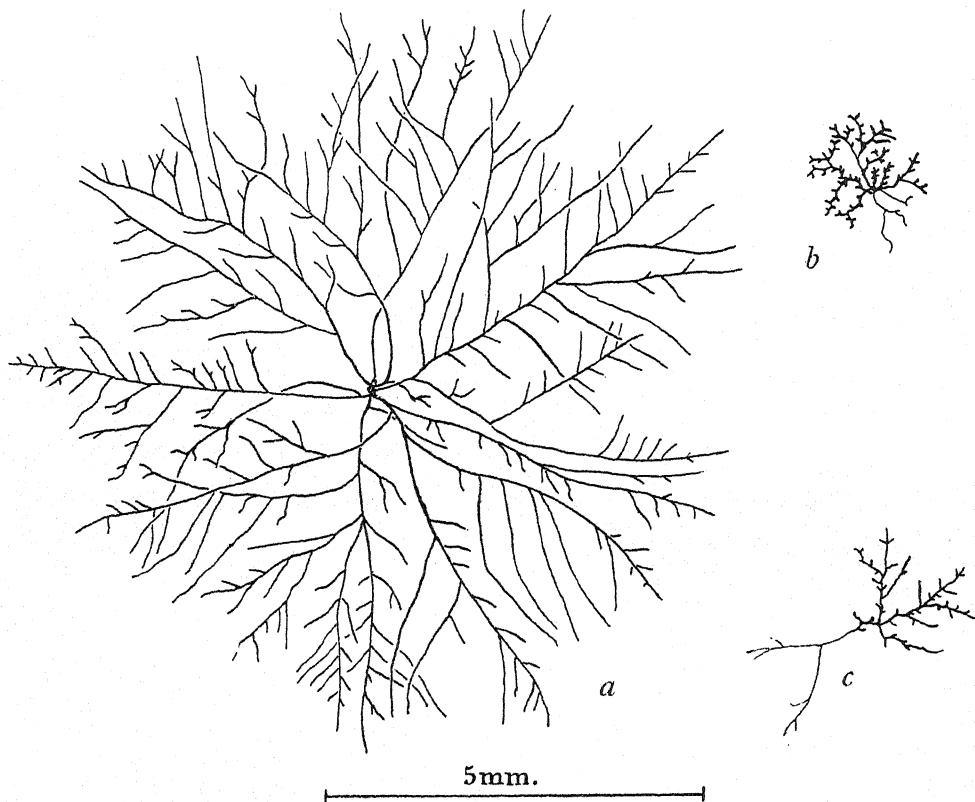
Series	Diameter, mm.		Remarks
	Whole colony	Fertile area	
C (normal)	22	12	<i>Edge.</i> Outline even, hyphae abundant, showing the usual regular branching
	23	12	<i>Centre.</i> Dense group of small head of sporangiola
	23	11	
M (large head)	18	4	<i>Edge.</i> Outline slightly uneven, hyphae looser than in C; branching showing vague pattern only
	17	3	
	18	3	<i>Centre.</i> Some sterile hyphae, strongly phototrophic. Heads beginning to form
DA	19	3	<i>Edge.</i> Outline even, hyphae rather crowded, no regular branching
DK (subnormal)	17	4	<i>Centre.</i> Low dense tuft with a few small heads
	21	9	<i>Edge.</i> Outline even, branching nearly as regular as controls
	23	10	
	22	9	<i>Centre.</i> Dense group of small heads, as in C. A few large sporangia only

(c) *Details of morphology and sporulation*

When the three variants were first isolated, they all grew more slowly than the parent form, and, to a greater or less extent, were distinguished by their lighter colour. They differed from normal *T. elegans*, and from one another, in the dimensions of the heads of sporangiola, and in the proportions in which sporangia and sporangiola were produced. It has been necessary in describing the behaviour of the forms in culture to make some reference to morphological features; these features will now be described in more detail. The drawings and photographs of *T. elegans* and of its variants which appear in this communication were taken from average examples of the objects they represent; they were not taken from specimens chosen to emphasise the differences between the normal and the variant forms.

(1) *The young colony.* Sporelings about twenty-four hours old are at a favourable stage for examination. Three sporelings of this age are

represented in Text-fig. 1; the normal sporeling shows already indications of the regular manner of branching characteristic of normal *T. elegans*; the spreading growth of this sporeling contrasts well with the stunted growth of the variant sporelings. The drawings were made when the variants had been in culture for two years and three months; the dwarf variant had retained the peculiar features of its sporelings



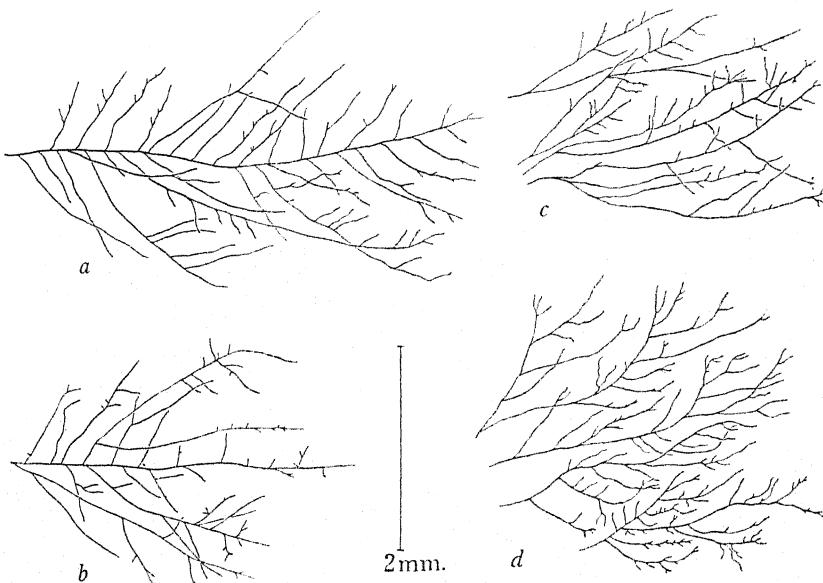
Text-fig. 1. *Thamnidium elegans*. Mycelia, 24 hours old, from single spores germinated on potato agar in dishes poured from the same lot of medium. *a*, normal form. *b*, the dwarf variant. *c*, the large-headed variant.

through fifty-four successive transfers, and the large-headed variant had done so through forty-eight transfers.

(2) *Branching in the growing edge of the colony*. The main hyphae of the normal strain spread evenly over the medium and branch in a regular fashion; the contrast between this regularity and the greater or less irregularity of the variants appears clearly in the photographs (Pl. XIV, figs. 8-10) and drawings (Text-fig. 2); a verbal description is

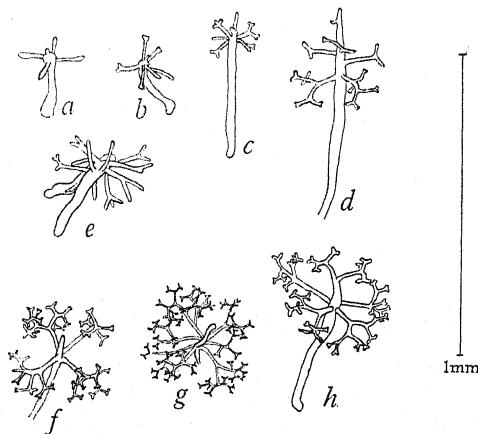
unnecessary. These hyphal characters are best investigated in cultures four to five days old, for, as the mycelium approaches the edge of the mycelium, branching becomes irregular, even in the ordinary form.

(3) *The fructifications.* The distinct aspects of cultures of normal *T. elegans* and of its variants were largely due to the differences in the diameters of the sporangiolic heads, due chiefly to the lengths reached by the successive branches of the dichotomising systems before they forked.

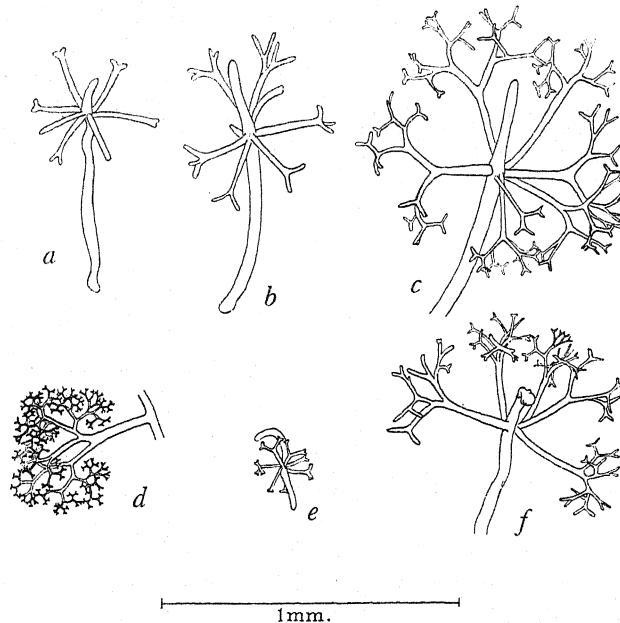


Text-fig. 2. *Thamnidium elegans*. Marginal hyphae from sister-cultures. *a*, normal form. *b*, the large-headed variant. *c, d*, the dwarf variant.

Almost all the heads of sporangiola in the dwarf variant (Text-fig. 3) were formed on short erect hyphae often less than a millimetre long. Very commonly, a whorl of four lateral branches arose a little below the tip of the hypha, these branches then forking several times and bearing the sporangiola on the tips of their ultimate ramifications. The tip of the main hypha did not always behave in the same way. Sometimes it persisted in a turgid and apparently healthy condition until the sporangiola contained ripe spores, but did not elongate. Sometimes the tip forked, each of the branches then forking two or three times, and eventually producing sporangiola. In other specimens, the tip grew on to form a tapering prolongation, from whose sides fertile branch systems or abortive attempts at fertile branch systems, might develop. Very frequently, the tip of the main axis



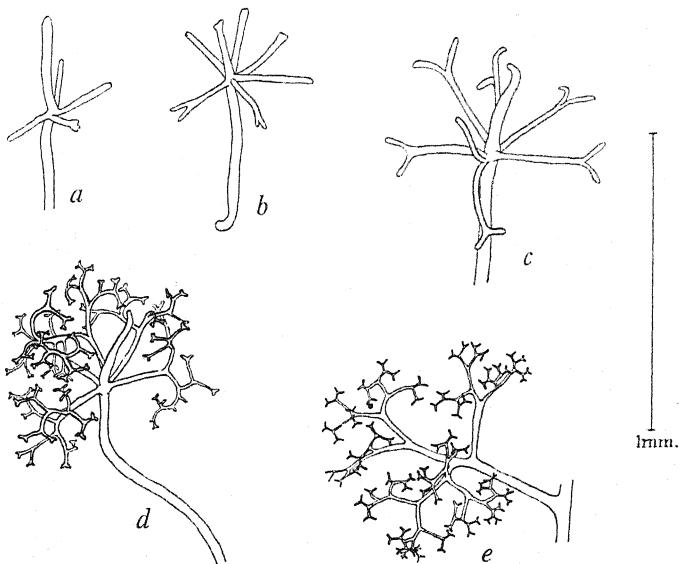
Text-fig. 3. *Thamnidium elegans*. Fertile heads of the dwarf variant. *a-e*, young stages. *f-h*, stages just before the development of sporangiola.



Text-fig. 4. *Thamnidium elegans*. Fertile heads of the normal form. *a-c*, young stages. *d*, one branch of a fertile head, just before the formation of sporangiola. *e*, young stage of a weak head, of the kind produced in very young cultures and towards the end of the period of growth. *f*, a head in course of formation, with the tip of the main hypha collapsing.

degenerated and either collapsed or persisted as a tiny papilla crowning a slight swelling of the axis. Rarely, the tip grew on, the lengthening hypha bore one or more successive sporangiolic tufts, and a large sporangium was organised at the end of the main fertile axis. Most of the fructifications of the dwarf variant had a stunted and partially abortive appearance.

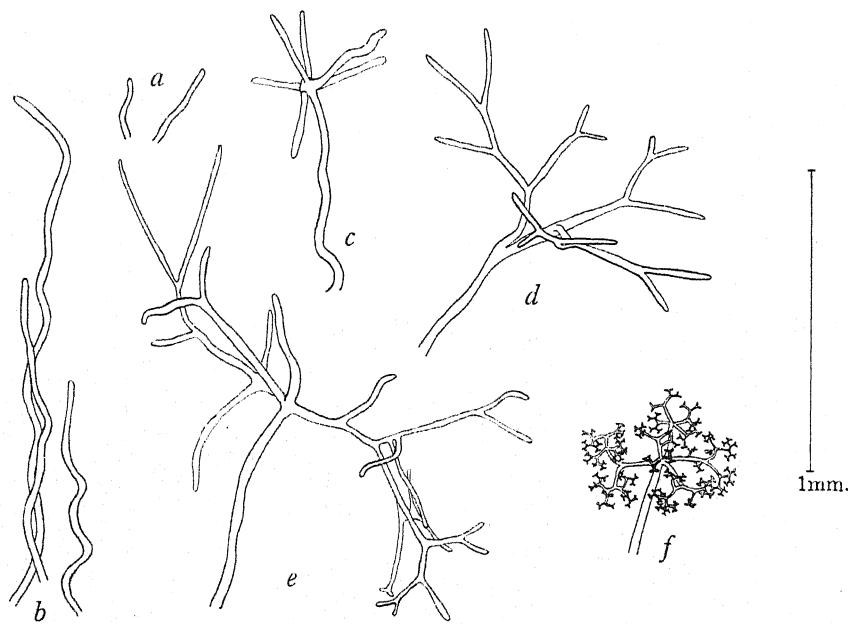
In cultures of the stock strain (Text-fig. 4 e), small terminal heads of sporangia developed, which in general characters were like the small heads usual in the dwarf variant. These heads however were



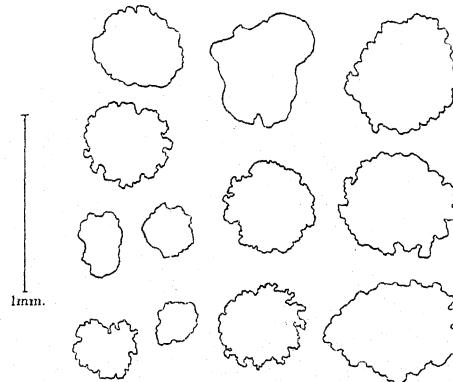
Text-fig. 5. *Thamnidium elegans*. Fertile heads of the large-headed variant. *a-d*, young stages. *e*, one branch of a fertile head, just before the formation of sporangiola, for comparison with Text-fig. 4*d*.

usually built up around at least five lateral branch systems, and they had a more robust appearance than those of the dwarf variant.

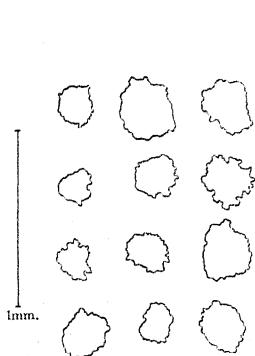
The sporangiolic heads (Pl. XIII, fig. 6, and Text-figs. 5 and 6) of the large-headed variant owed their size to the length of their constituent branches rather than to more extensive dichotomy. They probably bore no more sporangiola than average heads of the normal form, but were looser in construction. The main fertile axes of the large-headed variant usually reached as great a length as those of normal *T. elegans*, and often ended in a large sporangium. In this variant, especially when the mycelium was approaching the edge of the medium, large sporangia formed in fair numbers on the ends of short, simple sporangiophores, and, at the same time, as in the



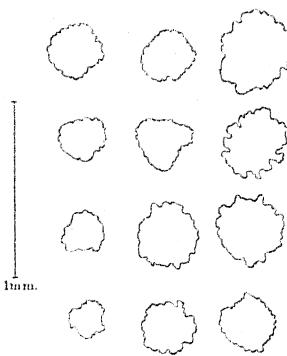
Text-fig. 6. *Thamnidium elegans*. The large-headed variant. a-b, weak aerial hyphae, usually strongly positively phototropic, and often remaining sterile. c-e, the sterile aerial branch systems characteristic of old cultures of the large-headed variant. f, a small fertile head, for comparison with Text-fig. 4e.



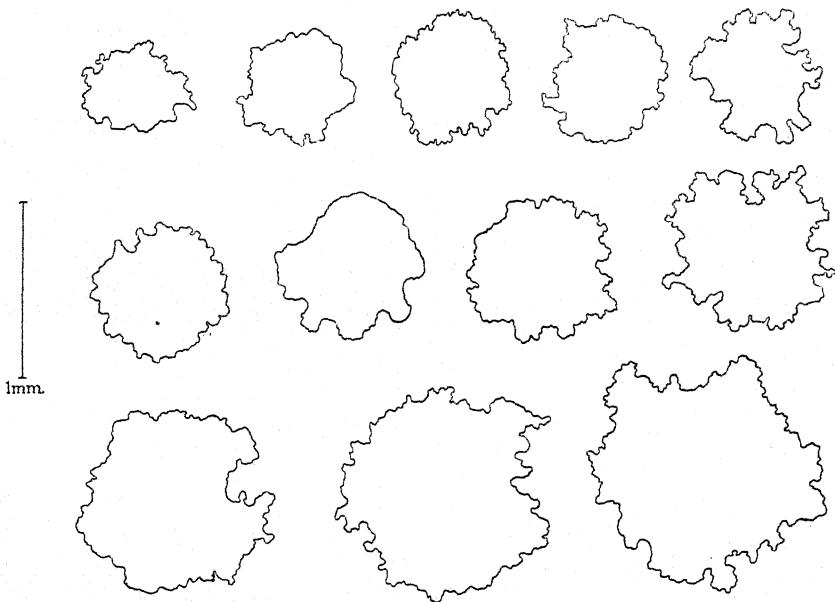
Text-fig. 7. *Thamnidium elegans*. Outlines of twelve heads of the normal form, chosen at random.



Text-fig. 8. *Thamnidium elegans*. Outlines of twelve heads of the dwarf variant, chosen at random.



Text-fig. 9. *Thamnidium elegans*. Outlines of twelve heads of the subnormal variant, chosen at random.



Text-fig. 10. *Thamnidium elegans*. Outlines of twelve heads of the large-headed variant, chosen at random.

ordinary form, heads of sporangiola were organised at the ends of short hypha (Text-fig. 6*f*): these heads showed the same looseness of construction as the lateral heads. In cultures of the large-headed variant about a fortnight old, a strong tendency became apparent for many of the branches in a sporangiolic tuft to fail to fructify, but to elongate and sometimes to bear lateral tufts of forking sterile branches in their turn (Text-fig. 6*d, e*). In old cultures, most samples taken for inspection contained all possible transitions from sporangiolic heads with every ultimate branchlet ending in a sporangium, to tufts of hyphae, evidently built up on a dichotomising system, but with only three or four dichotomies, and completely sterile.

Camera lucida tracings of the outlines of twelve heads of sporangiola from each of the four forms of *T. elegans* appear in Text-figs. 7-10. The twelve heads represented were chosen at random, the drawings being made from untouched living material in an unopened dish.

Although many samples were examined and measured, it was not possible to demonstrate any constant difference in form or in dimensions between the spores of normal *T. elegans* and of its variants.

#### THE NUMBER OF SPORES IN THE SPORANGIOLA

From time to time, counts have been made of the number of spores in the sporangiola of the various forms. In order to get fair sampling, the following method was used. Ripe tufts of sporangiola were mounted in water, and the slide was moved by means of the

Table V. Spore contents of sporangiola of *Thamnidium elegans*

Form of <i>T. elegans</i>	Normal	Subnormal	Dwarf	Large head
No. of sporangiola examined ...	3500	3500	3500	9000
Percentage of sporangiola with spore content of				
0	—	—	—	0.32
1	2.51	0.43	4.80	12.87
2	30.77	11.00	25.71	47.90
3	57.74	32.06	46.57	30.08
4	12.66	27.80	17.51	6.58
5	1.88	14.08	4.06	1.46
6	0.34	8.08	0.83	0.49
7	0.08	4.31	0.31	0.19
8	—	1.14	0.11	0.05
9	—	0.66	0.08	0.02
10	—	0.17	—	0.01
11	—	0.08	—	—
12	—	0.11	—	—
13	—	0.02	—	—
14	—	—	—	—
15	—	—	—	—
16	—	0.02	—	—

mechanical stage so that a number of separate strips of the preparation were examined. The spores lying in the uninjured sporangia which crossed an eyepiece scale between graduations 4 and 6 were counted. Counts were made from detached sporangiola, and from sporangiola still attached to their hyphae. On each occasion, the contents of five hundred sporangiola of each form of *Thamnidium elegans* were counted, the material being taken from cultures of the same set, generally about a fortnight old. The results of these counts, expressed in the form of percentages, are given in Table V.

The four forms of *Thamnidium elegans* evidently fall into two groups, one, including normal, subnormal and dwarf, with three-spored sporangiola predominating, the other including the large-headed variant only, with two-spored sporangiola predominating. In the three-spored group, the normal form alone is a constant one, for the two variants have gradually reverted towards it. The large-headed variant has remained consistently abnormal, retaining its light colour and its peculiarities of behaviour and morphology. The three-spored condition in normal *T. elegans* does not agree altogether with the statements in the literature that the sporangiola of *T. elegans* most often contain four spores. The stock strain used in this work may possibly be abnormal in its tendency to produce less than four spores in most of its sporangiola. As however Corda(6), van Tieghem and Le Monnier(14), Fischer(10) and other authors who have described *T. elegans* do not indicate the number of counts on which their statements are based, the possible abnormality in the stock strain is not regarded as established. Even if that abnormality exists, there is no doubt that the stock strain is of great constancy. The evidence of constancy afforded by behaviour during a long period of culture, and by frequent examinations of the morphological features of the strain, is strongly supported by the results of counts of the number of spores in the sporangiola. These counts are set out in detail in Table VI; they show that no significant alteration has occurred during the period 1929-33.

Table VI. Spore contents of sporangiola of normal *Thamnidium elegans*

No. of sporangiola with spore content of	Date of observation							Total
	1. x.	31. x.	22. ix.	2. xii.	16. ii.	20. i.	24. ii.	
1	13	14	33	12	3	10	3	88
2	176	169	170	176	109	153	124	1077
3	218	277	257	262	255	268	274	1811
4	81	33	35	44	104	63	83	443
5	9	7	4	6	22	3	15	66
6	2	—	1	—	5	3	1	12
7	1	—	—	—	2	—	—	3

Table VII. Spore contents of sporangiola of the subnormal variant of *Thamnidium elegans*

No. of sporangiola with spore content of	Date of observation							Total
	1. x.	31. x.	22. ix.	2. xii.	16. ii.	20. i.	24. ii.	
1	2	2	—	2	—	—	9	15
2	17	30	7	53	43	107	128	385
3	60	108	102	157	192	302	201	1122
4	98	156	178	178	159	82	122	973
5	104	100	113	75	69	7	25	493
6	102	54	62	25	28	1	11	283
7	70	34	30	6	6	1	4	151
8	22	9	6	2	1	—	—	40
9	15	3	2	2	1	—	—	23
10	4	2	—	—	—	—	—	6
11	1	1	—	—	1	—	—	3
12	3	1	—	—	—	—	—	4
13	1	—	—	—	—	—	—	1
14	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	—
16	1	—	—	—	—	—	—	1

The details of the counts made of the number of spores in the sporangiola of the subnormal variant contrast in an interesting manner with the counts relating to the normal form; they appear in Table VII. The drift towards normality shown by the subnormal form in culture is equally apparent in the production of spores in the sporangiola of successive cultures. It will be remembered that, when first recognised, the subnormal variant was specially characterised by the abundant development of large sporangia on short sporangiophores; this peculiarity in the constitution of the subnormal variant undoubtedly influenced the numbers in which spores developed in the sporangiola. In the early cultures, as a comparison of Tables VI and VII shows, there were great differences in this respect between the normal and subnormal forms. The divergence became less in later cultures, but, even at the beginning of 1933, over three years after the subnormal variant was taken into culture, the agreement in the counts of spores contained in the sporangiola of the normal and subnormal forms was not, perhaps, quite close enough to justify a conclusion that the subnormal variant had completely reverted to normal.

#### Characters of the large sporangia

The large sporangia appear to be alike in the normal form and in the variants. Measurements of the diameters of 1500 large sporangia taken from a number of cultures at intervals during the period of the investigation, revealed no significant differences in this character. Morphological variations were not noted.

#### CONCLUDING REMARKS

The results of the experiments with *T. elegans* confirm those previously obtained with *Eurotium herbariorum* and *Botrytis cinerea*. Variants appear in cultures from heated spores in numbers large enough to be significant, though, when the results of experiments with heated spores are compared with those of experiments in which X-rays have been used to provoke change (8, 9, 11), it is evident that, as a means of causing variation, the use of high temperatures is comparatively unproductive. Probably the point at which change occurs is close to the thermal death point.

It is not proposed to survey here the large volume of published work that now exists on induced variation. A number of investigators have successfully induced more or less permanent variations in both animals and plants, by the use of X-rays, ultra-violet light, radium, chemicals and relatively high temperatures. The results of experiments of this kind cannot be dismissed as due to faulty technique or to the selection of abnormalities already present in the stock. The variants of *T. elegans* were certainly not obtained by mere selection. If the normal stock was liable to vary, variants should have appeared sometimes in the large number of control cultures made during the investigation; they could never be found in control cultures, young or old. The spores of the established variants germinate without difficulty and without special treatment, and without a lag sufficient to allow the normal form to overgrow the variant sporelings; consequently there is no reason to suppose that the germination of the abnormal spores is favoured by a preliminary exposure to high temperatures. Direct experiment shows that normals and variants will grow side by side when planted in the same dish, each preserving its characters and remaining recognisable in dry cultures months or years old.

The variants are best regarded as weakened versions of normal *T. elegans*, damaged by the preliminary heating. In two, the damage appears to have been such that it could be slowly repaired during a long period of culture; these variants have been able to make a close approach to the normal state, if not to resume it completely. Temporary variants of this kind, even if able to persist for a long time in culture, cannot be regarded as possible sources of new species or varieties, though, were they found wild, they would probably be described as such.

The third variant has remained distinct, and may be a permanent form. This, the large-headed variant, is distinguished by its tendency to develop sporangiola with a small spore content, and to bear sterile branches in the sporangiolic heads. These characters, in a more pronounced form, are among the characters which separate *Thamnidium*

and *Chaetocladium*, so that, in these respects, we have an interesting parallel between the sort of changes that may occur under conditions of experiment, and the changes that may have occurred during the evolution of the Mucorales.

Savulescu and Rayss<sup>(13)</sup> have shown that spores of *Nigrospora Oryzae* may give rise after treatment at high temperatures to stunted progeny, but these investigators did not determine if the changed characters were transmitted to subsequent cultures. Their observations support the suggestion that colonies derived from heated spores are damaged versions of the parent form.

The changes produced in *T. elegans* did not affect all parts of the variants with the same intensity. The dwarf variant showed strong alteration of the vegetative system, and reduction in the size of the fructifications. The subnormal variant differed from normal chiefly in the formation of many large sporangia on short hyphae. The large-headed variant was specially distinguished by the production of loosely constructed heads with many sporangiola containing less than the normal average number of spores. It may be an accident, but it is interesting that the variant most altered in its fructification is also the most permanent of the variants investigated.

Modifications in *T. elegans*, directly related to the conditions of nutrition, have been observed by several investigators<sup>(1, 5, 7, 14)</sup>. Of these, Brefeld alone suggested that the modifications were transmissible. He stated that alterations in the proportions in which the two sorts of sporangia were produced could be brought about by the use of thin or thick sowings of spores, and that the changes could be increased by repetitions of the treatment. Bachmann<sup>(1)</sup> was unable to confirm this. Tests made with the normal stock used in the present work showed that colonies developed in the same way whether started from one or from many spores; variations could not be induced by adjusting the density of the inoculum.

The variants of *T. elegans* grown from heated spores preserved their distinctive features when grown side by side in dishes poured from the same lot of potato agar; it is therefore evident that nutritive conditions were not responsible for the development of the special characters of the variants, nor for the persistence of these characters in series of cultures.

Numerous attempts were made to obtain zygospores, by growing the four forms of *T. elegans* in contrasted cultures; all failed. The induced changes in morphology and cultural behaviour were not accompanied by any change in sexual reaction.

The experimental results show that *T. elegans* can be induced to yield variant forms when the spores are exposed to relatively high temperatures for a short time, and then planted under ordinary conditions, but it is not yet possible to obtain a given variant at will. In

this respect the results of the experiments agree with those of other workers who have induced changes in a variety of organisms by the use of physical and chemical agents.

#### SUMMARY

1. Spores of *T. elegans* have yielded variant cultures, after exposure to moderately high temperatures.
2. The variants have preserved their distinguishing characters through a considerable number of transfers. Of three variants described in detail, one was still quite distinct from the normal form after having been in culture for more than three years.

#### ACKNOWLEDGMENT

The provision of a microscope by the Government Grant Committee of the Royal Society is gratefully acknowledged.

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## EXPLANATION OF PLATES XIII AND XIV

## PLATE XIII

*Thamnidium elegans* Link.

Fig. 1. The large-headed variant.

Fig. 2. The normal form.

Fig. 3. The dwarf variant.

The cultures were grown side by side on dishes of potato agar poured from the same flask of medium; they were six days old when photographed. These cultures belonged to set 23, and the variants had been in culture for six months.

Figs. 4-5. The large-headed variant and the normal form, in cultures 21 days old. The cultures were sister cultures, and the variant had been in culture for a year, having passed through 35 transfers. The two cultures were photographed on the same plate, and the figures reproduced here were cut out from one print.

Fig. 6. Heads of the large-headed variant, showing the loose construction.  $\times 40$ .

Fig. 7. Heads of the dwarf variant as they appeared for some months after the variant was isolated,  $\times 100$ . The photograph was taken from a culture like that shown in Fig. 3.

## PLATE XIV

Figs. 8-10. Marginal hyphae of the large-headed variant, the normal form and the dwarf variant respectively,  $\times 60$ . The width of the hyphae is exaggerated by fluid lying against them.

Figs. 11-13. Portions of cultures of the large-headed variant, the normal form and the dwarf variant, photographed when the investigation had been in progress for a year. By this time, the dwarf variant had increased in strength, and was producing a fair number of well formed heads of sporangiola.  $\times 20$ .

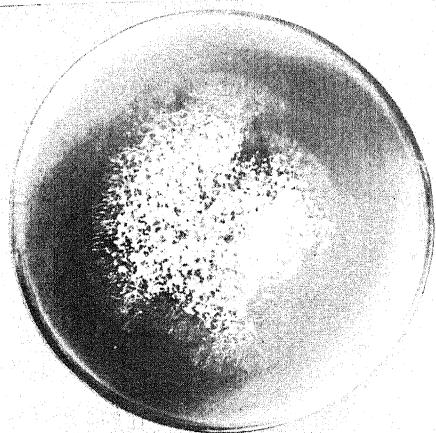


Fig. 1

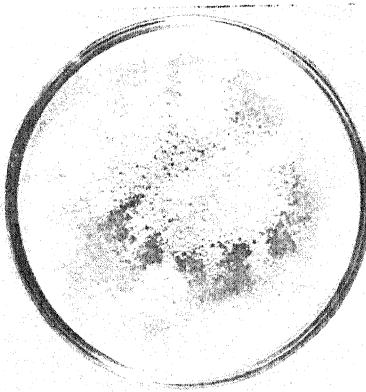


Fig. 4

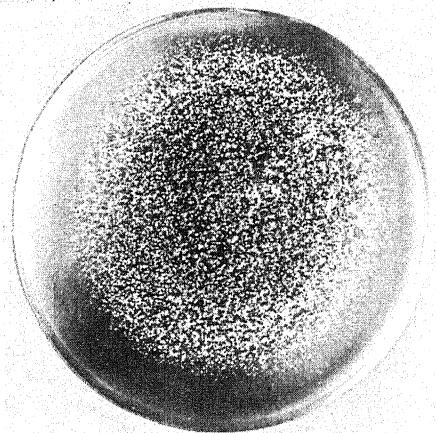


Fig. 2

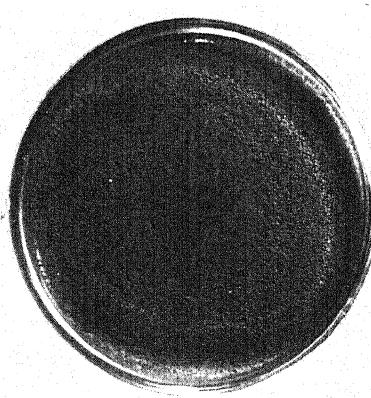


Fig. 5

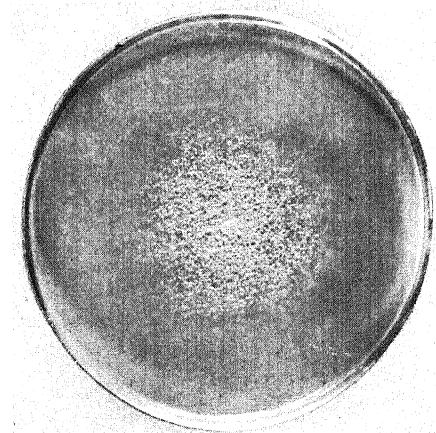


Fig. 3



Fig. 6

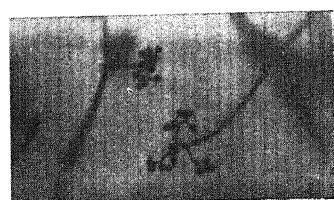


Fig. 7





Fig. 8

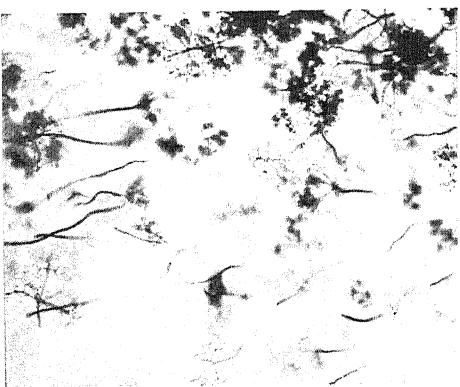


Fig. 11

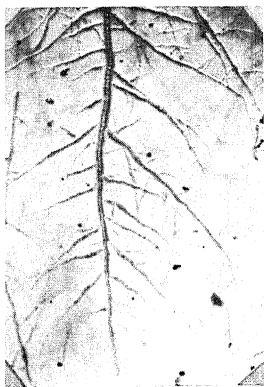


Fig. 9

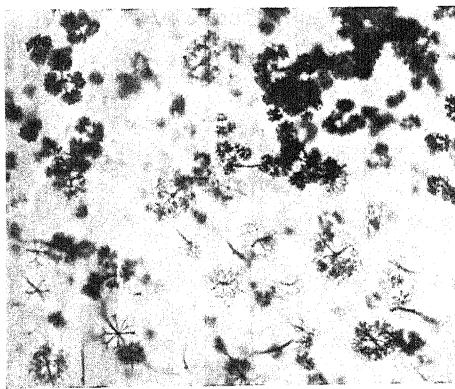


Fig. 12

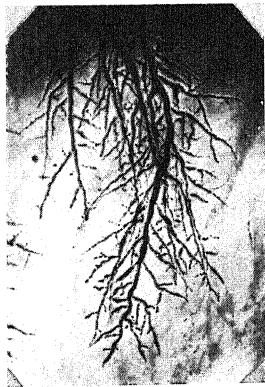


Fig. 10

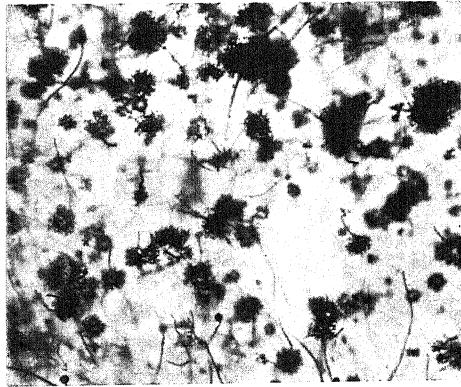
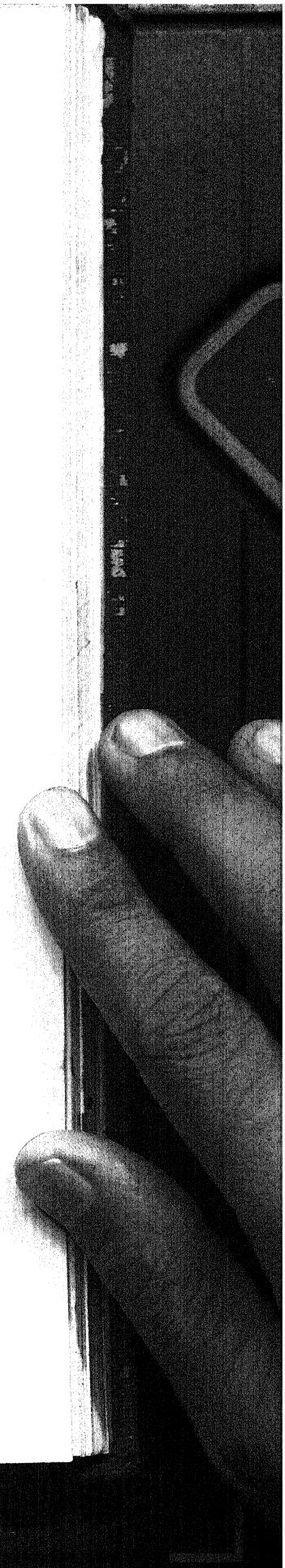


Fig. 13





## A LIST OF FUNGI, ETC., MAINTAINED IN THE NATIONAL COLLECTION OF TYPE CULTURES, 1935

BY R. ST JOHN-BROOKS AND MABEL RHODES

DURING the five years that have elapsed since the publication of the last list of fungi, etc., maintained in the National Collection of Type Cultures<sup>(1)</sup> many new types have been added to the collection and, it is thought, the time is now opportune for the issue of a new and revised catalogue. The list of cultures here published comprises some twelve hundred different species of fungi and bacteria as compared with some seven hundred and seventy species listed in these *Transactions* in 1930. Among the many sources from which the collection has been enriched during this period special reference may be made to the large series of *Aspergillus* and *Penicillium* species, etc., lodged for maintenance by Prof. H. Raistrick, which were employed by him and his co-workers in their studies in the biochemistry of micro-organisms<sup>(2)</sup>. These comprise some two hundred and twenty types, of which a considerable number are here listed; they are distinguished by the letters "R.C."

Early last year a working arrangement was made with the Director and staff of the Forest Products Research Laboratory, Princes Risborough, Bucks, whereby the extensive collection of wood-destroying fungi, and fungi causing discolouration in timber conserved by them, was made available for listing in the publications of the National Collection. This collection comprises some one hundred and eighty separate species, which are distinguished in the following list by the letters "F.P.R.L." Any applications for such lignicolous fungi received by the staff of the National Collection will be referred to the Forest Products Research Laboratory, who will deal with them direct. A small charge of 2s. 6d. per culture, which in some cases might be waived, will be made.

A complete reference to the bacteriological and mycological collection of the Bureau, as constituted in 1931, will be found in the catalogue published by the Medical Research Council in that year<sup>(3)</sup>. A new and revised edition of this catalogue is in course of preparation and, it is hoped, will be published this year. It will naturally include bacteria of medical and veterinary importance, which are outside the scope of the present publication.

Following the recommendations of the Nomenclature Committee of the International Society for Microbiology, of which the Curator

of the National Collection is one of the permanent secretaries, the use of the specific name "*Bacillus*" has been restricted in the following list to spore-bearing bacteria. A pronouncement on this subject has already been made by the Committee and the publication of their report has been promised for an early date in the *Zentralblatt für Bakteriologie*. Most of the non-sporing bacteria have been listed, without prejudice, under "*Bacterium*", others under "*Lactobacillus*", "*Acetobacter*", etc.

The Nomenclature Committee also appointed a subcommittee to report on the taxonomy and nomenclature of the *Salmonella* group of "food-poisoning" organisms. The results of their labours, which however do not necessarily express the views of the Committee, are embodied in a report recently published in the *Journal of Hygiene* (4).

The reference numbers of the cultures maintained in the collection should be quoted in all applications for type cultures, for which a small charge will be made, in most cases, to cover the cost of media, packing and postage. Organisms that do not appear on the list will be procured for correspondents, if available elsewhere. It is hoped that colleagues at home and abroad will continue to support the collection both by requests for cultures and by the deposit of important strains for maintenance and reference. It is requested that all communications be addressed to The Curator, National Collection of Type Cultures, Lister Institute, Chelsea Bridge Road, London, S.W. 1.

- 2791 *Absidia capillata* v. Tiegh.
- 1790 *A. coerulea* Bain.
- 3098 *A. glauca* (+) Hagem
- 3099 *A. glauca* (-) Hagem
- 2792 *A. Regnери* (Lucet & Cost.) Lendl.
- 1345 *Acetobacter aceti* (Hansen) Holland
- 2224 *A. acetosum* (Henneberg) Bergey et al.
- 3924 *A. Kuetzingianum* (Hansen) Bergey et al.
- 613 *A. Pasteurianum* (Hansen) Beij.
- 3734 *A. suboxydans* Kluyver & de Leeuw
- 4112 *A. xylinum* (A. Br.) Bergey et al.
- 3015 *Achorion Gallinae* (Mègnin) Saibour.
- 3013 *A. gypseum* Bodin
- 3011 *A. Quinckeum* Zopf
  - A. Schoenleinii. See *Grubyella*
- 3012 *A. violaceum* Bloch.
- 3826-3833 *Achromobacter* Bergey et al. spp. from slimy meat
- 706 *Acladium Castellani* Pinoy
- 3145 *Acremoniella olivaespora* Cif. & Ashf.
- 1268 *Acrostalagmus cinnabarinus* Corda
- 3146 *Acrotheca obovatum* var. *subcapitatum* Cif. & Ashf.
- 2958 *Acrothecium lunatum* Wakker
- 2393 *Actinomyces africanus* (Piper & Pullinger) Westerdijk
- 3526 *A. albido-flavus* (Rossi Doria)
- 1578 *A. albosporous* Kr.
- 3525 *A. albus* (Rossi Doria)
- 3258 *A. asteroides* (Eppinger) Gasp.
- 1574 *A. aureus* Waks. & Curt.
- 3440 *A. bovis* Wolff & Israel (anaerobic)
- 600 *A. bovis* Harz (aerobic)
- 3558 *A. cacaoi* I Waks.
- 3559 *A. cacaoi* II Waks.
- 3560 *A. cacaoi* III Waks.
- 1561 *A. californicus* Waks. & Curt.
- 659 *A. caprae* (Silb.) Lieske
- 3527 *A. carneus* (Rossi-Doria)
- 1934 *A. caviae* (Snijders)
- 1569 *A. chromogenus* Gasp.
- 2300 *A. coelicolor* (Reiner Müller) Lieske
- 1652 *A. corallinus* (Heff.)
- 1935 *A. Cuniculi* (Snijders)
- 803 *A. Dassonvillei* (Broque-Rousseau) Westerdijk

1564 *A. Fradii* Waks. & Curt.  
 1583 *A. griseus* Kr.  
 1585 *A. Lipmannii* Waks. & Curt.  
 576 *A. luteus* (Christoph. & Arch.) Westerdijk  
 3255 *A. madurae* (Vincent) Lehm. & Neum.  
 3026 *A. Pelletieri* (Laveran) Westerdijk  
 1566 *A. pheochromogenus* Conn.  
 2744 *A. praecox* Millard & Burr  
 2391 *A. pretorianus* (Pijper & Püllinger)  
 1565 *A. reticuli* Waks. & Curt.  
 1555 *A. reticulus-ruber* Waks.  
 2781 *A. ruber* (Carab.)  
 1562 *A. rutgersensis* Waks. & Curt.  
 1356 *A. scabies* (Thaxter) Güssow  
 2745 *A. Setonii* Millard & Burr  
 3236 *A. somaliensis* (Brumpt)  
 3524 *A. sulphureus* Gasp.  
 2392 *A. transvalensis* (Pijper & Püllinger)  
 2543 *A. tumuli* Millard & Beeley  
 1567 *A. violaceus-ruber* Waks. & Curt.  
 2746 *A. viridis* Millard & Burr  
 1580 *A. virido-chromogenus* Kr.  
 1554 *A. 96* Waks.  
 1582 *A. 104* Waks.  
 1584 *A. 128* Waks.  
 1586 *A. 145* Waks.  
 1581 *A. 168* Waks.  
 1560 *A. 206* Waks.  
 1571 *A. 218* Waks.  
 658 *A. sp.* Birt-Leishman (human pathogen)  
 1870 *A. sp.* from Dhobie itch  
 630 *A. sp.* from foal  
 450 *A. sp.* Gibson (human pathogen)  
 1676 *A. sp.* Rangoon (human pathogen)  
*Aerobacillus* Donker. See *Bacillus*  
 3249 *Allescheria Boydii* Shear (human pathogen)  
*A. Gayonii*. See *Eurotiopsis*  
 2863 *Alternaria Citri* Ellis & Pierce  
 2964 *A. macrospora* Zimm.  
 2925 *A. Solani* (Ell. & Mart.) Jones & Grout  
 4467 *A. tenuis* Nees  
 4090-4092 *A. spp.*, R.C.  
 605 *Amylomyces* sp. from tapioca  
 1314 *Anthostomella destruens* Shear  
*Aplanobacter* E. F. Smith. See *Bacterium*  
 4004 *Aposphaeria violacea* Bertel  
 4255 *Armillaria mellea* (Vahl) Fr., F.P.R.L.  
 4256 *A. mucida* (Schrad.) Fr. F.P.R.L.  
 3323 *Ascobolus furfuraceus* Pers.

1945 *Aspergillus Amstelodami* (Mang.) Thom & Ch.  
 595 *A. candidus* Link  
 1325 *A. carbonarius* (Bain.) Thom  
 3774 *A. cinnamomeus* Schiem., R.C.  
 978 *A. clavatus* Desm.  
 3775 *A. conicus* Bloch., R.C.  
 3776 *A. disjunctus* Bain. & Sart., R.C.  
 973 *A. effusus* Tiraboschi  
 3777 *A. ferrugineus* Fuck. (*A. glaucus* gr.), R.C.  
 3778 *A. ficuum* (Reich.) Henn. (*A. niger* gr.), R.C.  
 3779 *A. Fischeri* Wehm., R.C.  
 3890 *A. flavipes* Bain. & Sart., R.C.  
 596 *A. flavus* Link  
 1693 *A. fumaricus* Wehm.  
 982 *A. fumigatus* Fres.  
 3780 *A. giganteus* Wehm., R.C.  
 2655 *A. glaucus* group (Ascosporic)  
 1017 *A. luchuensis* Inui  
 3782 *A. medius* Meiss., R.C.  
 3783 *A. minimus* Wehm. (*A. glaucus* gr.), R.C.  
 3784 *A. mollis* Bain. & Sart. (*A. glaucus* gr.), R.C.  
 795 *A. nidulans* (Eidam) Winter  
 3786 *A. nidulans* (Eidam) Winter var. *Nicolleti* Pinoy, R.C.  
 594 *A. niger* v. Tiegh.  
 1692 *A. niger-citricus* Wehm.  
 979 *A. ochraceus* Wilh.  
 3787 *A. Okazakii* Okazaki, R.C.  
 598 *A. Oryzae* (Ahlb.) Cohn  
 3788 *A. ostianus* Wehm., R.C.  
 975 *A. parasiticus* Speare  
 1324 *A. pulverulentus* (McAlp.) Thom  
 3789 *A. repens* (Cda.) Sacc., R.C.  
 4155 *A. restrictus* Smith  
 4156 *A. restrictus* Smith var. B  
 3790 *A. Scheelei* Bain. & Sart., R.C.  
 2044 *A. Schiemannii* (Schiem.) Thom  
 980 *A. Sydowii* (Bain. & Sart.) Thom & Ch.  
 599 *A. tamarii* Kita  
 981 *A. terreus* Thom  
 974 *A. terricola* March. var. *americanus* March.  
 3757 *A. ustus* (Bain.) Thom & Ch., R.C.  
 3791 *A. versicolor* (Vuill.) Tiraboschi, R.C.  
 3792 *A. violaceo-fuscus* Gasp., R.C.  
 597 *A. Wentii* Wehm.  
 3925-3932 *A. spp.* (white), R.C.  
 2050 *Atelosaccharomyces* sp. Guilliermond

4184 *Azotobacter agilis* Beij.  
 1855 *A. chroococcum* Beij.  
 4229 *Azygozymum chladodosporum*  
     Chesters  
 3322 *Bacillus acetoethylicus* (Northrop)  
     *B. acetonigenus* (Donker) Thay-  
     sen. See *B. pectinovorus*  
 2604 *B. adhaerens* Laubach  
 4254 *B. aerothermophilus* Weinzirl  
 2598 *B. agri* Laubach & Rice  
 2601 *B. albolactis* Migula  
 3324 *B. alvei* Cheshire & Cheyne  
 2870 *B. aminovorans* den Dooren de  
     Jong  
 2590 *B. aterrimus* Lehm. & Neum.  
 2264 *B. Beijerinckii* (Donker)  
 2611 *B. brevis* Migula  
     619 *B. butylicus* Weizm.  
 1650 *B. butyricus* Hueppe (aerobe)  
     *B. butyricus* Prasmowski (an-  
     aerobe). See *B. Pasteurianus*  
 3716 *B. butyricus-iodophilus* Svartz  
 2690 *B. calidolactis* Hussong & Hammer  
 2599 *B. cereus* Frankland & Frankland  
 2600 *B. cereus* Fr. & Fr. var. *fluor-  
     escens* Laubach  
 2610 *B. circulans* Jordan  
 2584 *B. closteroides* Gray & Thorn.  
 2596 *B. cohaerens* Gottheil  
     927 *B. dendroides* Holzmüller  
 2121 *B. distortus* (Duclaux)  
 3472 *B. esterificans* Maassen  
 3220 *B. felsineus* Carbone & Tom-  
     bolato  
 3461 *B. filamentosus* Cozzolino  
 2120 *B. filiformis* (Duclaux)  
 2608 *B. fusiformis* Gottheil  
 2123 *B. geniculatus* (Duclaux)  
 2593 *B. Globigii* Migula  
 2689 *B. kaustophilus* Prickett  
 3879 *B. lactis* Flügge  
 3427 *B. lactomorbi* Jordan & Harris  
 3388 *B. larvae* White  
 2613 *B. laterosporus* Laubach  
 3223 *B. macerans* Schardinger  
 2605 *B. megaterium* de Bary  
     *B. megatherium*. See *B. mega-  
     terium*  
 2589 *B. mesentericus* (Flügge) Lehm.  
     & Neum.  
 2595 *B. mesentericus* (Flügge) L. & N.  
     var. *flavus* Laubach  
     *B. mesentericus fuscus*. See *B.  
     mesentericus*  
     *B. mesentericus niger*. See *B.  
     aterrimus*  
     *B. mesentericus panis viscosi*. See  
     *B. panis*  
     *B. mesentericus ruber*. See *B.  
     Globigii*  
     *B. mesentericus vulgatus*. See *B.  
     vulgatus*  
 4435 *B. methanigenes* Lehm. & Neum.  
 2122 *B. minimus* (Duclaux)  
 2602 *B. mycoides* Flügge  
 2736 *B. niger* Migula  
 2594 *B. panis* Migula  
 1649 *B. Pasteurianus* (Winogr.)  
 2263 *B. pectinovorus* (Beij. & van  
     Delden)  
 2606 *B. petasites* Gottheil  
 1380 *B. polymyxa* (Prazm.) Migula  
 2603 *B. Prausnitzii* Trevisan  
 2609 *B. pseudotetanicus* (Kruse) Migula  
 2116 *B. scaber* (Duclaux)  
 2597 *B. simplex* Gottheil  
 3610 *B. subtilis* (Ehrerb.) Cohn (type  
     strain)  
 2587 *B. subtilis-viscosus* Chester  
 1116 *B. tenuis* (Duclaux)  
 2612 *B. terminalis* Migula  
 2688 *B. terminalis* Migula var. *thermo-  
     philus* Prickett  
 3991 *B. thermoacidurans* Berry  
 3992 *B. thermoacidurans* Berry var. *a*  
     Berry  
 3993 *B. thermoacidurans* Berry var. *b*  
     Berry  
 2812 *B. thermophilus* Nègre  
 1490 *B. Truffautii* Truffaut & Bez-  
     sonoff  
 2607 *B. tumescens* Zopf  
 2588 *B. vulgatus* (Flügge) Migula  
     413 *Bacterium acidi-lactici* Hueppe  
     *B. acidophilum*. See *Lactobacillus*  
 1804 *B. acridiorum* (d'Herelle)  
 2872 *B. aminovorans* (den Dooren de  
     Jong)  
 2870A *B. aminovorans*  $\alpha$  (den Dooren  
     de Jong)  
 2870B *B. aminovorans*  $\beta$  (den Dooren  
     de Jong)  
 2871 *B. aminovorans*  $\gamma$  (den Dooren de  
     Jong)  
 2872 *B. aminovorans*  $\delta$  (den Dooren de  
     Jong)  
 3681 *B. amylovorum* (Burrill) Ser-  
     binoff  
 3682 *B. angulatum* Fromme & Murray  
 1977 *B. aptatum* N. R. Br. & Jamieson  
 1987 *B. aroideae* (Townsend) Stapp  
 1986 *B. atrofaciens* McCullough  
 1953 *B. atrosepticum* (van Hall)  
 303 *B. Barkeri* (St. J.-B.) Elliott  
 2797 *B. bifidum* (Tissier)  
 4473 *B. brunneum* Copeland

B. bulgaricum. See *Lactobacillus*  
2314 *Bacterium "C"* Chaston Chapman  
2029 *B. campestre* (Pammel) E. F. Smith  
1956 *B. Cannae* Bryan  
1975 *B. carotovorum* (Jones)  
1381 *B. caryocyaneum* (Beij.)  
408 *B. cloacae* Jordan  
4143 *B. coli-anindolicum* Lembke  
86 *B. coli-commune* Esch.  
419 *B. communius* (Durham)  
3683 *B. coronafaciens* Elliott  
3193 *B. costatum* (Cranston & Lloyd)  
2580 *B. cruciviae* (Gray & Thorn.)  
2572 *B. cycloclastes* Gray & Thorn.  
4031 *B. Delphinii* (E. F. Smith) Bryan  
1636 *B. denitrificans* (Burri & Stutz)  
1385 *B. denitrofluorescens-liquefaciens* Kluyver  
2578 *B. desmolyticum* Gray & Thorn.  
1356 *B. fluorescens-liquefaciens* Flügge  
912 *B. fluorescens-nonliquefaciens* Lehm. & Neum.  
3875 *B. fluorescens-putidum* Flügge  
3735 *B. Freundii* Braak  
1174 *B. fulvum* Zimm.  
2687 *B. globiforme* Conn  
661 *B. Guentheri* Lehm. & Neum.  
2880 *B. herbicola* Burri & Duggeli  
387 *B. Hyacinthi* Wakker  
2847 *B. indicum-rubrum* (Koch)  
2760 *B. indoloxidans* (Gray)  
2575 *B. iopagum* Gray & Thorn.  
3693 *B. Juglandis* (Pierce) E. F. Smith  
4252 *B. lachrymans* E. F. Smith & Bryan  
418 *B. lactis-aerogenes* Esch.  
3233 *B. lactis-viscosum* (Adametz) Lehm. & Neum.  
3441 *B. Lathyri* (Manns & Taubenhau)  
3224 *B. lipolyticum* Evans  
4248 *B. Malvacearum* (E. F. Smith) E. F. Smith  
1981 *B. marginale* N. A. Br.  
4469 *B. mazuni* Weigmann, Gruber & Huss  
4239 *B. medicagenis* (Sackett) E. F. Smith var. *phaseolicola* (Burkholder) Link & Hall  
1962 *B. Michiganense* E. F. Smith. See *Corynebacterium*  
1966 *B. Mori Boy.* & Lam.  
3797 *B. mors-prunorum* (Worm.)  
2794 *B. mucosum-capsulatum* Fasching  
414 *B. neapolitanum* Emmerich  
2164 *B. noctuarum* White  
3325 *B. orpheus* White  
4141 *B. oxytocom-perniciosum* (Wysokovitsch)  
3691 *B. Panici* Elliott  
3324 *B. paratyphosum-alvei* (Bahr)  
2686 *B. parvulum* Conn  
3692 *B. Pelargoni* N. A. Br.  
3685 *B. Phaseoli* E. F. Smith  
3686 *B. Phascoli* E. F. Smith var. *sojense* Hedges  
1985 *B. phytophthorum* (Appel)  
2576 *B. pictorum* (Gray & Thorn.)  
2446 *B. prodigiosum* (Cohn) Lehm. & Neum.  
394 *B. proteamaculans* (Paine & Stansfield) Elliott  
4175 *B. proteus-mirabilis* (Hauser)  
401 *B. proteus-vulgaris* (Hauser)  
4176 *B. proteus-zenkeri* (Hauser)  
3687 *B. Pruni* (E. F. Smith)  
3370 *B. prunicola* (Worm.)  
1999 *B. pyocyaneum* (Flügge) Lehm. & Neum.  
2196 *B. radicicola* Beij.  
1376 *B. radiobacter* (Beij.) Löhnius  
2577 *B. rathonis* (Gray & Thorn.)  
1655 *B. rossicum* Kell.  
2796 *B. rubefaciens* Burr  
2026 *B. salmonicida* Emmerich & Weibel  
4249 *B. seminum* (Cayley) Stevenson  
3272 *B. solaniolens* (Paine)  
385 *B. solanisaprum* (Harrison)  
2165 *B. sphingidis* White  
1969 *B. Stewartii* (E. F. Smith) McCulloch  
3246 *B. syncyaneum* (Ehrenb.) Lehm. & Neum.  
2813 *B. synxanthum* Ehrenb.  
1974 *B. Syringae* (van Hall) E. F. Smith  
3689 *B. tabacum* Wolf & Foster  
2881 *B. tenuie* Ehrenb.  
392 *B. Tolaasii* (Paine) Elliott  
1983 *B. tracheiphilum* (E. F. Smith) Jones et al.  
1967 *B. trifoliorum* Jones et al.  
*B. truttae.* See *B. salmonicida*  
1976 *B. tumefaciens* Smith & Townsend  
1654 *B. ureae* Leube  
4244 *B. viridiflavum* Burkholder  
3727 *B. viridilividum* N. A. Br.  
3688 *B. vitians* N. A. Br.  
620 *B. volutans* Thaysen  
972 *Bacterium "X"* A. Br.  
3419 *B. sp., from Allium* sp., Matsumoto  
2143 *B. sp., from cutworm*, Pospolov  
933 *B. sp., denitrifying*

3197 *B.* sp., marine chromogenic, Lloyd  
 3418 *B.* sp., from "Pe-tsai", Matsumoto  
 3420 *B.* sp., from *Phalaenopsis* sp., Matsumoto  
 3275 *B.* sp., from turnip, *Nirula*  
*Bacteroides* Cast. & Chalmers.  
 See *Bacterium*  
 3100 *Basidiobolus ranarum* Eidam  
 1801 *Beauveria Bassiana* (Bals.) Vuill.  
 1659A *B. densa* (Link) Picard  
 2227 *B.* sp. aff. *densa*, fly, Ceylon  
 1142 *B. globulifera* (Speg.) Picard  
 2226 *B. stephanoderis* (Bally) Petch  
 2706 *Betacoccus arabinosaceus* Orla-Jensen  
 3128 *Blakeslea trispora* (+) Thaxter  
 3129 *B. trispora* (-) Thaxter  
 4463 *Blastodendron Flarerii* Red. & Cif.  
 3147 *B. intermedium* Cif. & Ashf.  
*Blastomyces*. See *Cryptococcus*  
*Blastomycoides dermatitidis*. See  
*Cryptococcus*  
*B. immitis*. See *Coccidioides*  
 2688A *B. tulanensis* Cast. (human  
 Pathogen)  
 2805 *Blepharospora cambivora* Petri  
 2523 *Bodinea violacea* (Bodin) Ota &  
 Langer.  
 4006 *Botryosporium diffusum* (Grev.)  
 Corda  
 1161 *B. longibrachiatum* (Oud.) Maire  
 852 *Botrytis cinerea* Pers.  
 1189 *B. cinerea* Pers., biological strain  
 (fig)  
 1075 *B. cinerea* Pers., biological strain  
 (quince)  
 2712 *B. narcissicola* Kleb.  
 1138 *B. Paeoniae* Oud.  
 2713 *B. polyblastis* Dowson  
 1496 *B. Tulipae* (Lib.) Hopk.  
 1832 *Boudiera Claussenii* Henn.  
 2811 *Brettanomyces Claussen* sp.  
 4145 *Byssochlamys fulva* Olliver &  
 Smith  
 2201 *Calonectria graminicola* B. & Br.  
 1740 *Candida breve* Berkh.  
*C. candida*. See *Monilia*  
 1739 *C. Chodatii* Berkh.  
 4457 *C. mycotoruloides* Red. & Cif.  
 2135 *Caseococcus* sp. Gorini  
*Cellulomonas* Bergey et al. See  
*Bacterium*  
 1603 *Cephalosporium Asteris* Dowson  
 1859 *C. longisporum* Petch  
 1145 *C. Sacchari* Butl. See *Fusarium*  
*moniliforme*  
 4470 *C. subverticillatum* Schulz. &  
 Sacc.  
 4480 *C. Stuehmeri* Schmidt & v.  
 Beyma  
 1131 *Cephalothecium roseum* Corda  
 2517 *Cercosporina Kikuchii* Matsu-  
 moto  
 1315 *Ceuthospora lunata* Shear  
 4007 *Chaetocladium Brefeldii* (+) v.  
 Tiegh. & le Monn.  
 4008 *C. Brefeldii* (-) v. Tiegh. & le  
 Monn.  
 4020 *Chaetomium convolutum* Chivers  
 3309 *C. panosum* Wallr.  
 4100 *C. sp.*, R.C.  
 3184 *Chalara mycoderma* Bonord.  
 3109 *Chlamydomyces Palmarum* (Cooke)  
 Mason  
 2801 *Choanephora Cucurbitarum* (+)  
 (B. & Rav.) Thaxter  
 2802 *C. Cucurbitarum* (-) (B. & Rav.)  
 Thaxter  
 3073 *Chromobacterium hibernicum*  
 Grimes  
 2537 *C. violaceum* Bergonzoni  
 2416 *C. viscosum* Grimes  
 1791 *Circinella minor* Lendl.  
 2793 *C. spinosa* v. Tiegh. & le Monn.  
*Citrobacter Werkman* & Gillan.  
 See *Bacterium*  
 606 *Citromyces B* Wehmer. See *Peni-  
 cillium glabrum*  
 1182 *Cladosporium fulvum* Cooke  
 2278 *C. herbarum* Link  
 2783 *C. Mansonii* Cast.  
 4079-4081 *C. spp.*, R.C.  
 3043 *Clasterosporium maydicum* Sacc.  
 4094-4095 *C. spp.*, R.C.  
*Clostridium Prazmowski*. See  
*Bacillus*  
 833 *Coccidioides immitis* Rixf. &  
 Gilchr. (human pathogen)  
*Cocco-bacillus*. See *Bacterium*  
 836 *C. sp.* from oyster  
 2145 *Coccus* sp. from cutworm. Pos-  
 polov.  
 555 *C. sp.* from Emmentaler cheese  
 4138 *C. sp.* Henrici, pleomorphic  
 3849 *Colletotrichum atramentarium*  
 (B. & Br.) Taub.  
 1947 *C. Camilliae* Mass.  
 3501 *C. gloeosporioides* (Penz.) Sacc.  
 1606 *C. Lindemuthianum* (Sacc.)  
 Bres.  
 1194 *C. linicola* Pethyb. & Laff.  
 1130 *C. phomoides* (Sacc.) Chester  
 4257 *Collybia fusipes* (Bull.) Berk.,  
 F.P.R.L.

4258 *C. velutipes* (Curt.) Fr., F.P.R.L.  
4259 *Coniophora cerebella* Alb. &  
Schwein., F.P.R.L.  
1948 *Coniothecium chromatosporum*  
*Corda*  
1768 *Coniothyrium convolutum* Horne  
& Horne  
4260 *Coprinus micaceus* (Bull.) Fr.,  
F.P.R.L.  
4261 *C. radians* (Desm.) Fr., F.P.R.L.  
4262 *Corticium radiosum* Fr., F.P.R.L.  
4214 *Corynebacterium filamentosum*  
H. L. Jensen  
4212 *C. helvolum* (Zimm.) Kisskalt &  
Berend.  
4213 *C. insidiosum* (McCulloch) var.  
saprophyticum H. L. Jensen  
4217 *C. michiganense* (E. F. Smith)  
H. L. Jensen var. saprophyticum  
H. L. Jensen  
4218 *C. nubilum* (P. & C. Frankland)  
H. L. Jensen var. nanum H. L.  
Jensen  
4215 *C. simplex* H. L. Jensen  
4216 *C. tumescens* H. L. Jensen  
3679 *Coryneum microstictum* B. & Br.  
var. Mali Kidd  
2075 *Cryptococcus Castellani* Re  
2787 *C. dermatitidis* Gilchr. & Stokes  
(human pathogen)  
767 *C. farciminosus* Rivolta & Micel-  
lone  
2077 *C. gracilloides* Cast.  
1492 *C. histolyticus* (Freeman & Weid-  
man)  
3599 *C. hominis* (Busse) Vuill.  
2577 *C. linguae-pilosae* (Raynard &  
Lucet) Vuill.  
1869 *C. macroglossiae* Cast.  
2772 *C. metaniger* Cast.  
885 *C. nasalis* (Harrison)  
3598 *C. neoformans* (Sanfelice) Vuill.  
2774 *C. pararoseus* Cast.  
4455 *C. Pinoyisimilis* Cast.  
4456 *C. Pinoyisimilis* Cast. var. *Citel-  
liana* Red. & Cif.  
2773 *C. rubrorugosus* Cast.  
2673 *C. sp.* Hildebrand strain  
4158 *C. sp.* Pijper  
2674 *C. sp.* Sax strain  
1792 *Cunninghamella echinulata* Thaxter.  
3101 *C. elegans* (+) Lendl.  
3102 *C. elegans* (-) Lendl.  
4263 *Cyathus striatus* (Huds.) Pers.,  
F.P.R.L.  
2511 *Cylindrocarpon* Mali (All.) Wr.  
1294 *Cytosporina ludibunda* Sacc.  
1184 *C. Ribis* P. Magn.

4264 *Daedalea biennis* (Bull.) Quél.,  
F.P.R.L.  
4265 *D. confragosa* (Bolt.) Fr., F.P.R.L.  
4266 *D. quercina* (Linn.) Fr., F.P.R.L.  
4267 *D. unicolor* (Bull.) Fr., F.P.R.L.  
4268 *Daldinia concentrica* (Bolt.) Ces.  
& de Not., F.P.R.L.  
477 *Debaryomyces globosus* Klöck.  
2059 *D. Klöckeri* Guill. & Péju  
3593 *D. Matruchoti* Grig. & Péju  
2048 *D. tyrocola* Konokotine  
Dematioid pullulans. See Pullu-  
laria  
1682 *Diaporthe perniciosa* March.,  
forma *Pruni* Cayley  
4009 *Didium aurantium*  
1474 *Diplodia natalensis* Evans  
1009 *Diplodiella* sp.  
1133 *Diplodina Lycopersici* (Cooke)  
Hollós  
Discomyces Rivolta. See *Actino-  
myces*  
4269 *Echinodontium tinctorium* E. &  
H., F.P.R.L.  
1766 *Eidamia catenulata* Horne &  
Williamson  
1765 *E. tuberculata* Horne & Jones  
1764 *E. viridescens* Horne & Williamson  
703 *Endodermophyton indicum* Cast.  
1758 *E. tropicale* Cast.  
Endomyces. See *Endomycopsis*  
3592 *E. Magnusii* Ludwig  
3603 *Endomycopsis bisporus* (Beck)  
Dekker  
1871 *E. fibuliger* (Lindn.) Dekker  
1908 *E. fibuliger* (Lindn.) Dekker var.  
Hordei Saito  
2045 *E. fibuliger* (Lindn.) Dekker var.  
Lindneri Saito  
3601 *E. javanensis* (Klöck.) Dekker  
3602 *E. Mali* (Lewis) Dekker  
2241 *E. vernalis* (Ludwig) Dekker  
4068-4099 *Epicoccum* spp., R.C.  
2780 *Epidermophyton cruris* Cast.  
3016 *E. Pernetii* Cast.  
702 *E. rubrum* Cast.  
3579 *E. simii* Pinoy  
3310 *Eremascus fertilis* Stoppel  
Erwinia Winslow et al. See *Bac-  
terium*  
Escherichia Cast. & Chalmers.  
See *Bacterium*  
4270 *Favolus canadensis* Klotz., F.P.R.L.  
4271 *Fistulina hepatica* (Huds.) Fr.,  
F.P.R.L.  
4272 *Flammula sapinea* Fr., F.P.R.L.  
Flavobacterium Bergey et al. See  
*Bacterium*

4273 *Fomes annosus* Fr., F.P.R.L.  
 F. *applanatus*. See *Ganoderma*  
 4275 *F. conchatus* (Pers.) Fr., F.P.R.L.  
 4276 *F. connatus* Fr., F.P.R.L.  
 4277 *F. ferruginosus* (Schrad.) Massee,  
 F.P.R.L.  
 4278 *F. fraxineus* (Bull.) Fr., F.P.R.L.  
 4279 *F. fraxinophilus* (Peck.) Sacc.,  
 F.P.R.L.  
 4280 *F. igniarius* (Linn.) Fr., F.P.R.L.  
 4281 *F. juniperinus* Schrenk, F.P.R.L.  
 4282 *F. Laricis* (Jacq.) Murrill, F.P.R.L.  
 4283 *F. nigricans* Fr., F.P.R.L.  
 4284 *F. pinicola* (Sw.) Cke., F.P.R.L.  
 2169 *F. pinicola* (Sw.) Cke. var.  
*marginalis*  
 4285 *F. pomaceus* (Pers.) Big. Guill,  
 F.P.R.L.  
 4286 *F. Ribis* (Schum.) Fr., F.P.R.L.  
 4287 *F. rimosus* Berk., F.P.R.L.  
 4288 *F. robustus* Karst., F.P.R.L.  
 4289 *F. roseus* (A. & S.) Fr., F.P.R.L.  
 4290 *F. scutellatus* Schwein., F.P.R.L.  
*F. tinctorium*. See *Echinodontium*  
 4291 *F. vinosus* Berk., F.P.R.L.  
 3505 *Fragosphaeria purpurea* Shear  
 4373 *Fumago vagans* Pers.  
 1770 *Fusarium acuminatum* (Ell. &  
 Ev.) Wr.  
 2710 *F. avenaceum* (Fr.) Sacc.  
 3793 *F. bulbigenum* Cke. & Mass.  
 1141 *F. coeruleum* (Lib.) Sacc.  
 2709 *F. culmorum* (W. G. Sm.) Sacc.  
 2735 *F. culmorum* (W. G. Sm.) Sacc.  
 var. *leteius* Sherb.  
 1136 *F. Dianthi* Prill. & Del.  
 4062 *F. falcatum* App. & Wr., R.C.  
 3097 *F. fructigenum* Fr.  
 2711 *F. herbarum* (Corda) Fr.  
 2862 *F. javanicum* Koorders  
 2509 *F. juruanum* P. Henn  
 1081 *F. Lini* Bolley  
 1767 *F. Malli* Taub.  
 4054 *F. Martii* App. & Wr., R.C.  
 4067 *F. metachroum* App. & Wr., R.C.  
 3794 *F. moniliforme* Sheld., R.C.  
 4069 *F. orthoceras* App. & Wr., R.C.  
 4071 *F. oxysporum* Schl., R.C.  
 4066 *F. rhizophilum* Corda, R.C.  
 4060 *F. Salicis* Fuck., R.C.  
 4064 *F. sambucinum* Fuck., R.C.  
 4070 *F. Scirpi* Lamb. & Fautr., R.C.  
 4053 *F. Solani* (Mart.) App. & Wr. var.  
 minus Fr., R.C.  
 1296 *F. sporotrichioides* Sherb.  
 4057 *F. trichotechiooides* Wr., R.C.  
 4058 *F. tubercularoides* (Corda) Sacc.,  
 R.C.

4056 *F. uncinatum* Wr., R.C.  
 1696 *F. vasinfectum* Atk.  
 3300 *F. vasinfectum* Atk. var. *aegypti-*  
*cum* Fahmy  
 4052 *F. viride* Wr., R.C.  
 4055-4068 *F. spp.*, R.C.  
 4292 *Ganoderma applanatum* (Pers.)  
 Pat., F.P.R.L.  
 4293 *G. lucidum* (Leyss.) Karst.,  
 F.P.R.L.  
 4294 *G. oregonense* Murr., F.P.R.L.  
 4295 *G. resinaceum* Boud., F.P.R.L.  
*Geotrichum immite*. See *Cocci-*  
*dioides*  
 4472 *G. javanense* Verona  
 4106 *Gibberella Saubinetii* (Mont.)  
 Sacc.  
 1454 *Gliocladium penicilliodes* Corda  
 1730 *G. roseum* Bain.  
 2513 *Gloeosporium fructigenum* Berk.  
 1797 *G. limeticola* Claussen  
 1390 *G. Musarum* Cke. & Mass.  
 1839 *G. nervisequum* (Fuck.) Sacc.  
 3552 *G. pestis* Mass.  
 1317 *Glomerella rufomaculans-Vaccinii*  
 Shear  
 1861 *Gonatorrhodiella coccorum* Petch  
*Granulobacter* Bei. See *Bacillus*  
 2527 *Grubyella Schoenleinii* (Lebert)  
 Ota & Langer.  
 3326 *Guignardia Vaccinii* Shear  
 3311 *Gymnoascus Reessii* Baran.  
 817 *Hansenia apiculata* (Reess) Lindn.  
 816 *H. apiculata* Schmitz  
 478 *Hanseniaspora valbyensis* Klöck  
*Hansenula*. See *Willia*  
 3551 *Haplosporangium bisporale* Thax-  
 ter  
 3877 *Helicostylum nigricans* v. Tiegh.  
 1793 *H. piriforme* Bain.  
 4010 *Helminthosporium Avenae* Eidam  
 4082 *H. geniculatum* Tracy & Earle,  
 R.C.  
 4087 *H. gramineum* Rabenh., R.C.  
 1319 *H. inaequale* Shear  
 4086 *H. interseminatum* Berk. & Rav.,  
 R.C.  
 1357 *H. Sacchari* Butl.  
 1888 *H. sativum* Pam., King & Bakke  
 4083 *H. teres* Sacc., R.C.  
 4085 *H. sp.*, R.C.  
 2778 *Hemispora pararugosa* Cast.,  
 Doug. & Thomp.  
 705 *H. rugosa* Cast.  
 2769 *H. stellata* Vuill.  
 2186 *Hendersonia Sacchari* Butl.  
 4088 *Heterosporium gracile* Sacc., R.C.  
 4089 *H. variable* Cke., R.C.

4296 *Hexagonia discopoda* Pat. & Hariot, F.P.R.L.  
 2893 *Hormodendrum Langeronii* da Fonseca, Leão & Penido  
 4297 *Hydnus coralloides* (Scop.) Fr., F.P.R.L.  
 4298 *Hypholoma fasciculare* Huds., F.P.R.L.  
 4299 *H. hydrophilum* (Bull.) Quél., F.P.R.L.  
 4300 *H. perplexum* (Peck) Dacc., F.P.R.L.  
 4301 *H. sublateritium* Schaeff., F.P.R.L.  
 4302 *H. velutinum* (Pers.) Fr., F.P.R.L.  
 3415 *Hypochnus sasakii* Shirai H. Solani. See *Rhizoctonia*  
 4303 *Irpea* destruens Petch, F.P.R.L.  
 4304 *I. obliquus* (Schrad.) Fr., F.P.R.L.  
 2957 *Isaria farinosa* (Dicks) Fr. Kloeckera Janke. See *Pseudosaccharomyces*  
 Kurthia Trevisan. See *Bacterium*  
 1320 *Lachnea abundans* (Karst.) Sacc.  
 3312 *L. cretea* (Cke.) Phill.  
 4034 *Lactobacillus acidophil-aerogenes* (Torrey & Rahe) Bergey et al.  
 1899 *L. acidophilus* (Moro) Holland  
 76B *L. bulgaricus* (Grigoroff) Holland  
 2375 *L. Delbrueckii* (Leichm.) Holland  
 4036 *L. fermentatae* Bergey et al.  
 4113 *L. helviticus* (Orla-Jensen) Bergey et al.  
 4035 *L. leichmannii* (Henneberg) Bergey et al.  
 4114 *L. lycopersici* Mickle  
 947 *L. pentoaceticus* Fred., Peterson & Davenport  
*L. plantarum*. See *Streptobacterium*  
 4305 *Lentinus cochleatus* (Pers.) Fr., F.P.R.L.  
 4306 *L. Lecomptei* Fr., F.P.R.L.  
 4307 *L. lepideus* Fr., F.P.R.L.  
 4308 *L. tigrinus* (Bull.) Fr., F.P.R.L.  
 4309 *Lenzites abietina* Bull., F.P.R.L.  
 4310 *L. betulina* (Linn.) Fr., F.P.R.L.  
 4311 *L. bicolor* Falck, F.P.R.L.  
 4312 *L. flaccida* Fr., F.P.R.L.  
 4313 *L. saeparia* (Wulf.) Fr., F.P.R.L.  
 4314 *L. trabea* Pers., F.P.R.L.  
 2170 *Leptothrix* sp. (human pathogen)  
 3739 *Leuconostoc citrovorum* (Hammer) Huck. & Ped.  
 3354 *L. dextranicum* (Beij.) Huck. & Ped.  
 3351 *L. mesenteroides* (Cienk.) v. Tiegh.

4315 *Lycoperdon pyriforme* (Schaeff.) Pers., F.P.R.L.  
 3677 *Macrophomma phaseoli* (Maubl.) Ashby  
 4474 *Macrosporium commune* Rabh.  
 2280 *M. sarcinula* Berk.  
 3235 *Madurella mycetomi* Brumpt  
 3027 *Malassezia Baillon* sp. from *Tinea flava*  
 3273 *Margarinomyces Bubakii* Laxa  
*Melanospora destruens*. See *Anthostomella*  
 2185 *M. pampeana* Speg.  
 1862 *M. parasitica* Tul.  
 3704 *Memnoniella echinata* (Riv.) Galloway  
 4316 *M. Merulius corium* Fr., F.P.R.L.  
 4317 *M. lachrymans* (Wulf.) Fr., F.P.R.L.  
 4318 *M. minor* Falck., F.P.R.L.  
 4319 *M. sclerotiorum* Falck., F.P.R.L.  
 4320 *M. serpens* (Tode) Fr., F.P.R.L.  
 4321 *M. sylvester* Falck, F.P.R.L.  
 1660 *Metarrhizium anisopliae* (Metsch.) Sor.  
 2676 *Micrococcus agilis* Ali-Cohen  
 1630 *M. aurantiacus* Cohn  
 1657 *M. candidans* Flügge  
 4161 *M. caseolyticus* Evans  
 1628 *M. concentricus* Zimm.  
 2677 *M. conglomeratus* Migula  
 1629 *M. flavus* (Flügge) Lehm. & Neum.  
 2679 *M. Freudenreichii* Guillebeau  
 3873 *M. lactis-viscosus* Sternberg  
 2680 *M. luteus* (Schröt.) Cohn  
 2665 *M. lysodeikticus* Fleming  
 2558 *M. piltonensis* Gray & Thorn.  
 2682 *M. rhodochrous* Zopf.  
 1114 *M. roseus* (Bumm.) Lehm. & Neum.  
 2559 *M. sphaeroides* Gray & Thorn  
 1631 *M. sulphureus* Zimm.  
 951 *M. tetragenus* Koch & Gaffky  
 2684 *M. ureae* Cohn  
 2685 *M. varians* Migula  
 3090 *Microcyclus aquaticus* Ørskov  
 3853 *Micromonospora chalceae* (Fouerten) H. L. Jensen  
 3856 *M. coerulea* H. L. Jensen  
 3854 *M. fusca* H. L. Jensen  
 3855 *M. parva* H. L. Jensen  
 1749 *Microspira agarliquefaciens* Gray & Chalmers  
*Microsporum Audouini*. See *Sabouraudites*  
 3008 *M. equinum* Bodin  
 3009 *M. ferrugineum* Ota  
*M. felineum*. See *Sabouraudites*

3007 *M. fulvum* Uriburu  
 2106 *M. Japon* Kambayashi  
 3313 *Monascus purpureus* Went  
 714 *Monilia albicans* (Robin) Zopf  
 2855 *M. Ashfordii* Cast.  
 2856 *M. butantanensis* Cast.  
 922 *M. candida* Bon.  
 2858 *M. fusca* Browne  
 2850 *M. javanica* Went. & Geer.  
 698 *M. krusei* Cast.  
 697 *M. macedoniensis* Cast.  
 2776 *M. metalondinensis* Cast.  
 2851 *M. nigra* Burri & Staub  
 2853 *M. parapsilosis* Ashf.  
 707 *M. Pinoyi* Cast.  
 2775 *M. pseudotropicalis* Cast.  
 2852 *M. psilosporus* Ashf.  
 3590 *M. sitophila* (Mont.) Sacc.  
 696 *M. tropicalis* Cast.  
 2755 *M. variabilis* Lindn.  
 4458 *M. zeylanoides* Cast.  
 2146 *M. sp.*, from "cutworm", Pos-  
 polov  
 2505 *M. sp.*, from tongue (human  
 pathogen)  
 3694 *Monosporium acuminatum* Bon.  
 v. *terrestris* Sacc.  
 3105 *Mortierella candelabrum* v. Tiegh.  
 & le Monn.  
 3150 *M. niveo-velutina* Cif. &  
 Ashf.  
 3106 *M. reticulata* v. Tiegh. & Le  
 Monn.  
 1903 *Mucor alternans* v. Tiegh.  
 1904 *M. erectus* Bain.  
 2010 *M. hiemalis* (+) Wehm.  
 2011 *M. hiemalis* (-) Wehm.  
 1901 *M. javanicus* Wehm.  
 1121 *M. lusitanicus* Brüderlein  
 3231 *M. Moelleri* Vuill.  
 3744 *M. Mucedo* (+) Linn.  
 3745 *M. Mucedo* (-) Linn.  
 1123 *M. plumbeus* Bon.  
 1902 *M. pusillus* Lindt  
 1122 *M. racemosus* Fres.  
 921 *M. Rouxi* Wehm.  
 1126 *M. sphaerosporus* Hagem  
 1821 *M. spinosus* v. Tiegh.  
*M. stolonifer*. See *Rhizopus*  
*nigricans*  
 4322 *Mycena galericulata* Scop.,  
 F.P.R.L.  
 2571 *Mycobacterium actinomorphum*  
 Gray & Thorn.  
 2562 *M. agrestis* Gray & Thorn.  
 1470 *M. album* Söhn  
 2570 *M. coeliacum* Gray & Thorn.  
 2568 *M. convolutum* Gray & Thorn.  
 2566 *M. crystallophagum* Gray &  
 Thorn.  
 4219 *M. equi* (Magnusson) H. L.  
 Jensen  
 2569 *M. erythropolis* Gray & Thorn.  
 2761 *M. globerulum* Gray  
 1472 *M. lactocola* Söhn.  
 1469 *M. luteum* Söhn.  
 2275 *M. marinum* Aronson  
 2874 *M. opacum* den Dooren de Jong  
 525 *M. Phlei* (Möller) Lehm. & Neum.  
 1471 *M. Phlei* Söhn.  
 4220 *M. rubro-pertinctum* (Heff.) Ford  
 1468 *M. rubrum* Söhn.  
 2873 *M. salmonicolor* den Dooren de  
 Jong  
 53 *M. smegmatis* (Alvarez & Tavel)  
 Lehm. & Neum.  
 526 *M. Stercoris* Bergey et al. (Möller's "Mist" Bacillus)  
 2071 *M. sp.* Karlinski  
*Mycocandida* Red. & Cif. See  
*Cryptococcus*  
 1849 *Mycoderma arborescens* Kuf-  
 ferath  
 1848 *M. Bordetii* Kufferath  
 819 *M. cerevisiae* Desm., Hansen  
 2055 *M. Chevalieri* Guill.  
 3021 *M. cutaneum* Ota (human patho-  
 gen)  
 3347 *Mycogone perniciosa* Magn.  
 2561 *Mycoplana bullata* Gray & Thorn.  
 2560 *M. dimorpha* Gray & Thorn.  
 4461 *Mycotorula dimorpha* Red. &  
 Cif.  
 1842 *M. famata* Harrison  
*M. Pinoyi*. See *Monilia*  
 4462 *M. trimorpha* Red. & Cif.  
 4460 *M. verticillata* Red. & Cif.  
 1843 *M. vesica* Harrison  
*M. zeylanoides*. See *Monilia*  
 3331 *Mystrosporium adustum* Massee  
 1846 *Nadsonia fulvescens* Syd.  
 1143 *Nectria diversispora* Petch  
 1795 *N. Ipomoeae* Hals.  
 3675 *Nematospora Coryli* Pegl.  
 3411 *N. Gossypii* Ashby & Nowell  
 3314 *Neocosmospora vasinfecta* E. F.  
 Smith  
 3411 *Neurospora crassa* Shear & Dodge  
 2500 *Nigrospora Oryzae* (B. & Br.)  
 Petch  
*Nocardia Trevisan*. See *Actino-*  
*myces*  
*Oidium albicans*. See *Monilia*  
 700 *O. asteroides* Cast.  
 2886 *O. lactis* Fres.  
 2777 *O. matalense* Cast.

701 *O. rotundatum* Cast.  
 3087 *O.* sp. Chaston Chapman (from factory effluent)  
 2103 *Omphalia flava* (Cke.) Maubl. & Rangel  
 3500 *Oospora Citri-aurantii* (Ferr.) Sacc. & Syd.  
 1742 *O. fragrans* (Kzr.) Berk. var. *minuta* Berk.  
 1743 *O. humi* (Mazé) Berk.  
 3532 *Paecilomyces hibernicum* Kenn. & Grimes  
 3089 *P. Varioti* Bain.  
 1241 *P.* sp. Segal  
 4323 *Panus stipticus* (Bull.) Fr., F.P.R.L.  
 4324 *P. torulosus* (Pers.) Fr., F.P.R.L.  
 1062 *Parasaccharomyces Ashfordii* Anderson  
 4325 *Paxillus panuoides* Fr., F.P.R.L.  
 3943 *Penicillium aurantio-violaceum* Biourge, R.C.  
 984 *P. avellaneum* Thom. & Tuesson  
 3956 *P. baculatum* West., R.C.  
 3940 *P. Biourgeianum* Zal., R.C.  
*P. brevicaule.* See *Scopulariopsis*  
*P. brevicaule* var. *album*. See *Scopulariopsis*  
 3568 *P. brevi-compactum* Dierckx  
 582 *P. camemberti* Thom.  
*P. camemberti* var. *Rogeri*. See *P. caseicola*  
*P. candidum* Roger & Mazé. See *P. caseicola*  
 583 *P. caseicola* Bain.  
 4154 *P. Charlesii* Smith  
 589 *P. chrysogenum* Thom  
 3539 *P. citrinum* Thom., R.C.  
 1718 *P. claviforme* Bain.  
 3974 *P. commune* Thom., R.C.  
 4039 *P. corymbiferum* Westl., R.C.  
 4002 *P. crustosum* Thom., R.C.  
 3800 *P. Daleae* Zal., R.C.  
 3947 *P. digatatum* Sacc., R.C.  
*P. divaricatum.* See *Paecilomyces Varioti*  
 587 *P. Duclaixii* Delacr.  
*P. elongatum.* See *P. tardum*  
 593 *P. expansum* Link  
 3975 *P. fusco-glaucum* Biourge, R.C.  
 3944 *P. glabrum* (Wehm.) Westl., R.C.  
 3994 *P. Gladioli* Machacek, R.C.  
*P. glaucum.* See *P. terrestris*  
 3977 *P. Godlewskii* Zal., R.C.  
 1720 *P. granulatum* Bain.  
 3565 *P. Hagemi* Zal.  
 1721 *P. herquei* Bain. & Sart.  
 3566 *P. hirsutum* Dierckx  
 3499 *P. italicum* Wehm.

4041 *P. kilense* Weidemann, R.C.  
 3973 *P. lanoso-coeruleum* Thom., R.C.  
 3972 *P. lanoso-viride* Thom., R.C.  
 3799 *P. lanosum* Westl., R.C.  
 584 *P. lilacinum* Thom  
 585 *P. luteum* Zukal  
 3958 *P. meleagrinum* Biourge, R.C.  
 4222 *P. notatum* Westl.  
 3971 *P. ochraceum* Bain.-Thom., R.C.  
*P. olivaceum.* See *P. digatatum*  
 983 *P. oxalicum* Currie & Thom  
 4151 *P. pallidum* Smith  
 1722 *P. patulum* Bain.  
 3936 *P. Pfefferianum* (Wehm.) Westl., R.C.  
 1151 *P. pinophilum* Hedcock  
 3968 *P. puberulum* Bain., R.C.  
 586 *P. purpurogenum* Stoll  
 4153 *P. Raistrickii* Smith  
 588 *P. roqueforti* Thom  
*P. roseum.* See *Gliocladium*  
 592 *P. rugulosum* Thom  
 4038 *P. Schneggii* Boas, R.C.  
 3029 *P. solitum* Westl.  
 4042 *P. spiculosporum* Lehman, R.C.  
 591 *P. spinulosum* Thom  
 3950 *P. Steckii* Zal., R.C.  
 1719 *P. tardum* Thom  
 3978 *P. terrestris* Jensen, R.C.  
 4152 *P. varians* Smith  
 3997 *P. verrucosum* Dierckx, R.C.  
 3567 *P. vesiculosum* Bain.  
 3998 *P. viridicatum* Westl., R.C.  
 4326 *Peniophora gigantea* Fr., F.P.R.L.  
 4327 *P. incarnata* (Pers.) Cke., F.P.R.L.  
 4328 *P. quericina* (Pers.) Cke., F.P.R.L.  
 4329 *P. sanguinea* (Fr.) Bres., F.P.R.L.  
 3276 *Periconia felina* E. March.  
 3680 *Pestalozzia Hartigii* Tubeuf.  
 1299 *P. Palmarum* Cooke  
 1259 *P. Theac* Sawada  
 3514 *P. versicolor* Speg.  
 4330 *Phebia merismoides* Fr., F.P.R.L.  
 3366 *Phialophora verrucosa* Medlar (human pathogen)  
 4331 *Pholiota adiposa* Fr., F.P.R.L.  
 4332 *P. albo-crenulata* Peck, F.P.R.L.  
 4333 *P. heteroclita* Fr., F.P.R.L.  
 4334 *P. lucifera* (Lasch.) Fr., F.P.R.L.  
 4335 *P. mutabilis* (Schaeff.) Quél., F.P.R.L.  
 4336 *P. spectabilis* Fr., F.P.R.L.  
 4337 *P. squarrosa* (Müll.) Fr., F.P.R.L.  
 1135 *Phoma alternariaceum* Brooks & Searle  
 1950 *P. Betae* Frank  
 2656 *P. Lingam* (Tode) Desm.  
 1798 *P. Pomi* Pass.

1088 *Phomopsis* sp. from plum  
 2653 *Photobacterium phosphorescens* (Fischer) Beij.  
 1383 *P. phosphorium* Beij.  
 2894 *Phycomyces nitens* (+) Kunze  
 2895 *P. nitens* (-) Kunze  
 1799 *Physalospora Cydoniae* Arnaud  
 3385 *P. Miyabeana* Fukushi  
*Phytomonas* Bergey et al. See *Bacterium*  
 2807 *Phytophthora Arecae* (Colem.) Pethyb.  
 3062 *P. Boehmeriae* Sawada  
 2082 *P. Cactorum* (Lib. & Cohn) Schröt  
 3061 *P. Capsici* Leon.  
 2804 *P. Cinnamomi* Rands  
 3057 *P. citricola* Saw.  
 3134 *P. Colocasiae* Rac.  
 2803 *P. cryptogea* Pethyb. & Laff.  
 2069 *P. erythroseptica* Pethyb.  
 1193 *P. Fagi* Hart.  
 3058 *P. hydrophila* Curzi  
*P. infestans* (Mont.) de Bary  
 2808 *P. Meadii* McRae  
 3550 *P. megasperma* Drechs.  
 3063 *P. melongenae* Saw.  
 1752 *P. palmivora* Butl.  
 3132 *P. palmivora* Butl., rubber group  
 3133 *P. palmivora* Butl., cacao group  
 2080 *P. parasitica* Dastur  
 2809 *P. Pini* Leon.  
 3299 *P. Porri* Forster  
 2806 *P. Richardiae* Buis.  
 3055 *P. Syringae* Kleb.  
 3060 *P. Tabaci* Saw.  
 481 *Pichia alcohophilica* Klöck.  
 483 *P. calliphorae* Klöck.  
 3594 *P. Chodati* (Zender) Dekker  
 3595 *P. Chodati* (Zender) Dekker var. *Trumppii* (Zender) Dekker  
 901 *P. farinosa* Lindn.-Hansen  
 3863 *P. hyalospora* Lindn.  
 479 *P. membranaefaciens* Hansen  
 480 *P. polymorpha* Klöck.  
 482 *P. suaveolens* Klöck.  
 4011 *Piptocephalis Freseniana* de Bary  
 3107 *P. sp.* Wilkins  
 3412 *Piricularia Oryzae* Cav.  
 3025 *Pityosporum rhinocerosum* Sabour.  
 3327 *Pleospora pomorum* Horne  
 1451 *Pleurage verruculosis* Jensen  
 4338 *Pleurotus euosmus* (Berk.) Cke., F.P.R.L.  
 4339 *P. lignatilis* Fr., F.P.R.L.  
 4340 *P. ostreatus* (Jacq.) Fr., F.P.R.L.  
 4341 *P. palmatus* (Bull.) Quél., F.P.R.L.  
 4342 *P. sapidus* Schulz., F.P.R.L.  
 4343 *P. ulmarius* Bull., F.P.R.L.  
 4344 *Pluteus cervinus* (Schaeff.) Fr., F.P.R.L.  
 1761 *Polyopeus aureus* Horne  
 3678 *P. purpureus* Horne var. *verus* Horne  
 4345 *Polyporus adustus* Fr., F.P.R.L.  
 4346 *P. albo-sordescens* Rom., F.P.R.L.  
 4347 *P. anceps* Peck, F.P.R.L.  
 4348 *P. balsameus* Peck, F.P.R.L.  
 4349 *P. benzoinus* (Wahlenb.) Fr., F.P.R.L.  
 4350 *P. Berkeleyi* Fr., F.P.R.L.  
 4351 *P. betulinus* (Bull.) Fr., F.P.R.L.  
 4352 *P. borealis* (Wahlenb.) Fr., F.P.R.L.  
 4353 *P. brumalis* (Pers.) Fr., F.P.R.L.  
 4354 *P. caesius* (Schrad.) Fr., F.P.R.L.  
 4355 *P. chioneus* Fr., F.P.R.L.  
 4356 *P. circinatus* Fr., F.P.R.L.  
 4357 *P. conchifer* Schwein., F.P.R.L.  
 4358 *P. croceus* (Pers.) Fr., F.P.R.L.  
 4359 *P. dryadeus* (Pers.) Fr., F.P.R.L.  
 4360 *P. dryophilus* (Berk.) var. *vulninus*, F.P.R.L.  
 4361 *P. elegans* (Bull.) Fr., F.P.R.L.  
 4362 *P. fragilis* Fr., F.P.R.L.  
 4363 *P. frondosus* Fr., F.P.R.L.  
 4364 *P. fumosus* (Pers.) Fr., F.P.R.L.  
 4365 *P. giganteus* (Pers.) Fr., F.P.R.L.  
 4366 *P. glivus* Schwein., F.P.R.L.  
 4367 *P. graveolens* Schwein., F.P.R.L.  
 4368 *P. guttulatus* Peck, F.P.R.L.  
 4369 *P. hispidus* (Bull.) Fr., F.P.R.L.  
 4370 *P. intybaceus* Fr., F.P.R.L.  
 4371 *P. lacteus* (Bull.) Fr., F.P.R.L.  
 4372 *P. nummularius* (Bull.) Quél., F.P.R.L.  
 4373 *P. orientalis* Lloyd, F.P.R.L.  
 4374 *P. picipes* Fr., F.P.R.L.  
 4375 *P. pubescens* (Schum.) Fr., F.P.R.L.  
 4376 *P. radiatus* (Sow.) Fr., F.P.R.L.  
 4377 *P. resinosus* (Schum.) Quél., F.P.R.L.  
 4378 *P. rutilans* (Pers.) Fr., F.P.R.L.  
 4379 *P. Schweinitzii* Fr., F.P.R.L.  
 4380 *P. sspumeus* (Sow.) Fr. var. *mongolicus* Murashk., F.P.R.L.  
 4381 *P. squamosus* (Huds.) Fr., F.P.R.L.  
 4382 *P. sulphureus* (Bull.) Fr., F.P.R.L.  
 4383 *P. rheades* Pers., F.P.R.L.  
*P. Tamariscis* (Pat.) Sacc. & D. Sacc. See *P. rheades*  
 4384 *P. tephroleucus* Fr., F.P.R.L.  
 4385 *P. Tsugae* (Murr.) Overholt, F.P.R.L.  
 4386 *P. tuberaster* Fr., F.P.R.L.

4387 *P. tulipiferus* (Schwein.) Overholt  
F.P.R.L.

4388 *P. varius* (Pers.) Fr., F.P.R.L.

4389 *P. vulpinus* Fr., F.P.R.L.

4390 *P. zonatus* (Nees) Fr., F.P.R.L.

1004 *Polyspora* Lini Laff.

4391 *Polystictus abietinus* (Dicks.) Fr.,  
F.P.R.L.

4392 *P. cinnabariensis*, F.P.R.L.

4393 *P. hirsutus* (Wulf.) Fr., F.P.R.L.

4394 *P. sanguineus* (L.) Mey., F.P.R.L.

4395 *P. versicolor* (Linn.) Fr., F.P.R.L.

4396 *Poria crassa* Karst., F.P.R.L.

4397 *P. ferruginea-fusca* Karst., F.P.R.L.

4398 *P. hypolateritia* Berk., F.P.R.L.

4399 *P. incrassata* (B. & C.) Burt.,  
F.P.R.L.

4400 *P. laevigata* Fr., F.P.R.L.

4401 *P. obducens* (Pers.) Fr., F.P.R.L.

4402 *P. punctata* Fr., F.P.R.L.

4403 *P. subacida* Peck, F.P.R.L.

4404 *P. tsugina*, F.P.R.L.

4405 *P. Vaillantii* (DC.) Fr., F.P.R.L.

4406 *P. vaporaria* (Pers.) Fr.,  
F.P.R.L.

4407 *P. xantha* Lind., F.P.R.L.

3489 *Proactinomyces minimus* H. L.  
Jensen

3488 *P. paraffinæ* H. L. Jensen

3486 *P. polychromogenes* (Vallee)  
H. L. Jensen

Proteus Hauser. See *Bacterium*

2875 *Protaminobacter albo-flavum*  $\alpha$   
den Dooren de Jong

2876 *P. albo-flavum*  $\beta$  den Dooren de  
Jong

2877 *P. albo-flavum*  $\gamma$  den Dooren de  
Jong

2878 *P. albo-flavum*  $\delta$  den Dooren de  
Jong

2879 *P. rubrum* den Dooren de Jong

3151 *Prototheca portoricensis* Cif. &  
Ashf.

3152 *P. portoricensis* Cif. & Ashf. var.  
*trispora* Cif. & Ashf.

*Pseudomonas* Migula. See *Bac-  
terium*

499 *Pseudosaccharomyces africanus*  
Klöck.

490 *P. antillarum* Klöck.

497 *P. apiculatus* (Hansen) Reess

492 *P. austriacus* Klöck.

485 *P. corticis* Klöck.

491 *P. germanicus* Klöck.

487 *P. indicus* Klöck.

498 *P. javanicus* Klöck.

494 *P. Jensenii* Klöck.

489 *P. Lafarii* Klöck.

1816 *P. Lindneri* Klöck.

484 *P. malaianus* Klöck.

496 *P. Muelleri* Klöck.

486 *P. occidentalis* Klöck.

493 *P. santacruzensis* Klöck.

488 *P. Willii* Klöck.

1745 *Pullularia nigra* Berk.

1547 *P. pullulans* (de Bary & Löw)  
Berk.

3317 *Pyronema confluens* Tul.

3053 *P. domesticum* (Sow.) Sacc.

3048 *Pythium acanthicum* Drechs.

3546 *P. anandrum* Drechs.

3328 *P. aphanidermatum* (Eds.) Fitz.

2810 *P. complectens* Braun

2467 *P. de Baryanum* Hesse

3557 *P. graminicola* Subram.

3545 *P. helicoides* Drechs.

3549 *P. intermedium* de Bary

3232 *P. irregulare* Buis.

3547 *P. periplocum* Drechs.

2652 *P. splendens* Braun

4408 *Radulum quercinum* Fr., F.P.R.L.

4096 *Rhacodium cellare* Pers.  
*Rhinocladium*. See *Sporotrichum*  
*Rhizobium* Frank. See *Bacterium*  
*Rhizoctonia bataticola*. See  
*Macrophomina Phaseoli*

1175 *R. destruens* Tassi

*R. lamellifera* Small. See *Macro-  
phomina Phaseoli*

1464 *R. Solani* Kühn

2097 *R. Tuliparum* (Kleb.) Whetzel

1905 *Rhizopus japonicus* Vuill.

3108 *R. nigricans* (+) Ehrenb.

2419 *R. nigricans* (-) Ehrenb.

1907 *R. Oryzae* Went & Geer.

1906 *R. tonkinensis* Vuill.

2466 *R. Tritici* Saito

907 *Rhodotorula plicata* Harrison

241A *R. rutila* Harrison

4409 *Rosellinia arcuata* Petch, F.P.R.L.

2526 *Sabouraudites Audouinii* (Gruby)  
Ota & Langer.

2524 *S. felineus* (Fox & Blaxall) Ota &  
Langer.

2525 *S. lanosus* (Sabour.) Ota &  
Langer.

3864 *Saccharomyces anamensis* Will &  
Heinrich

*S. apiculatus*. See *Pseudosac-  
charomyces*

3597 *S. Blanchardii* (Blanchard) Guiart

1808 *S. brasiliensis* Lindn.

742 *S. carlsbergensis* Hansen

3865 *S. cartilaginosus* Lindn.

815 *S. cerevisiae* Hansen (Baking  
yeast)

2160 *S. cereviseae* Hansen (Brewing yeast)  
 2779 *S. cereviseae* Hansen (Distilling yeast)  
 2054 *S. Chevalieri* Guill.  
 3964 *S. Delbrueckii*  
 467 *S. ellipsoideus* Hansen  
 3866 *S. ellipsoideus* Hansen var. cratericus  
 812 *S. exiguum* (Reess) Hansen  
 3139 *S. festinans* Ward & Baker  
 905 *S. fragilis* Jörgensen  
 1681 *S. Hansenii* Zopf  
 1809 *S. Illicis* Grönlund  
 469 *S. intermedium* Hansen  
 2053 *S. Lindneri* Guill.  
 472 *S. Marxianus* Hansen  
 743 *S. monacensis* Hansen  
 2049 *S. muentzii* (Kayser) Naganishi  
 468 *S. Pastorianus* Hansen  
*S. Pastorianus* II. See *S. intermedium*  
*S. Pastorianus* III. See *S. validus*  
 1071 *S. piriformis* Marshall Ward  
 1015 *S. sake* Yabe  
 790 *S. thermantitonum* Johnson  
 4203 *S. turbidans* Hansen  
 470 *S. validus* Hansen  
 2404 *S. sp.* from Californian wine  
 1879 *S. sp.* (Cider yeast)  
 3859 *S. sp.* (Fernbach 1)  
 3860 *S. sp.* (Fernbach 33)  
 3861 *S. sp.* (Fernbach 38)  
 3862 *S. sp.* (Fernbach 40)  
 3863 *S. sp.* (Fernbach 41)  
 903 *S. sp.* (Frohberg yeast)  
 3965 *S. sp.* (Hill's yeast)  
 1806 *S. sp.* (Yeast: Johannesberg II) Wörtmann  
 904 *S. sp.* (Kefir yeast) Hansen  
 607 *S. sp.* (Yeast: lactose-fermenting)  
 909 *S. sp.* (Logos yeast)  
 1639 *S. sp.* (Mahua yeast)  
 1467 *S. sp.* (Mineral yeast, "Futterhefe")  
 1346 *S. sp.* (Pink yeast)  
 3966 *S. sp.* (Race V)  
 2074 *S. sp.* (Rasse II)  
 2031 *S. sp.* (Rasse XII)  
 906 *S. sp.* (Saaaz yeast)  
 608 *S. sp.* (Sternberg yeast, "675")  
 473 *Saccharomyces* Ludwigii Hansen  
 814 *Saccharomyces* capsularis Schiönn.  
 3593 *Saprolegnia* sp.  
 952 *Sarcina aurantiaca* Flügge  
 3868 *S. flava* de Bary  
 3967 *S. gasoformans* Gruber  
 611 *S. lutea* Flügge  
 2768 *Scedosporium apiospermum* Sacc. (human pathogen)  
 4410 *Schizophyllum commune* Fr., F.P.R.L.  
 1014 *Schizosaccharomyces* mellacei Jörg.  
 382 *S. octosporus* Beij.  
 902 *S. Pombe* Lindn.  
 476 *Schwanniomyces* occidentalis Klöck.  
 1073 *Sclerotinia cinerea* Schr.  
 1238 *S. cinerea* Schr. forma Mali Wormald  
 1239 *S. cinerea* Schr. forma Pruni Wormald  
 2198 *S. erythronii* Whetzel  
 1072 *S. fructigena* (Pers.) Schr.  
 3342 *S. intermedia* Ramsay  
 3343 *S. minor* Jagger  
 1074 *S. sclerotiorum* (Lib.) Bref.  
 3344 *S. trifoliorum* Erikss.  
 1076 *Sclerotium cepivorum* Berhk.  
 2516 *S. fulvum* Fr.  
 2714 *S. Gladioli* Massey  
 1262 *S. Rolfsii* Sacc.  
 1497 *S. Tuliparum* Kleb.  
 2965 *Scolecobasidium constrictum* Abbott  
 580 *Scopulariopsis brevicaulis* (Sacc.) Bain.  
 581 *S. brevicaulis* (Sacc.) Bain. var. alba Thom  
 3171 *S. sp.* from Bullfrog  
 3867 *S. sp.* from Numbskull toad  
 1891 *Septoria Lycopersici* Speg.  
 1594 *S. Tritici* Desm.  
*Serratia Bizio.* See *Bacterium*  
 3318 *Sordaria fimicola* (Rab.) Ces. & de Not.  
 3319 *S. sp.* Wilkins  
 4072 *S. sp.* R.C.  
 2864 *Sphaeropsis malorum* Peck  
 3068 *Sphaerostilbe aurantiaca* Tub.  
 1860 *Spicaria javanica* Bally  
 2229 *S. prasina* (Maubl.)  
 953 *Spirillum rubrum* v. Esmarch  
 1750 *Spirochaeta cytophaga* Hutch.  
 2959 *Spondylocladium xylogenum* A.L. Smith  
 3533 *Sporendonema casei* Desm.  
 4179 *Sporidinia grandis* Link  
 3770 *Sporodesmium Bakeri* Syd.  
 3017 *Sporotrichum Beurmannii* Matr. & Ram.  
 4075 *S. bombycinum* (Corda) Rab.  
 4074 *S. carneolum*

1672 *S. carnis* Brooks & Hansford  
 4157 *S. Carougeauii* Langer.  
 3020 *S. equinum*  
 3019 *S. Gougerotii* Matr.  
 406 *S. Schenckii* Perkins  
 193 *Staphylococcus cereus-flavus* Pas-  
     set  
 963 *S. cremoris-viscosi* Hammer &  
     Cordes  
 3769 *Stemphylium macrosporoideum*  
     (B. & Br.) Sacc.  
 1005 *S. sp.* from cotton canvas  
 1455 *S. sp.* from soil  
 4411 *Stereum fasciatum* (Schw.) Fr.,  
     F.P.R.L.  
 4412 *S. hirsutum* Fr., F.P.R.L.  
 4413 *S. purpureum* Fr., F.P.R.L.  
 4414 *S. rugosum* (Pers.), F.P.R.L.  
 4415 *S. sanguinolentum* (Alb. & Schw.)  
     F.P.R.L.  
 4416 *S. spadiceum* Fr., F.P.R.L.  
 4417 *S. spadiceum* Fr. var. *quercinum*  
     Fr., F.P.R.L.  
     *Sterigmatocystis* Cramer. See *As-  
         pergillus*  
 3253 *Streptobacterium casei* Orla-Jen-  
     sen  
 4125 *S. plantarum* Orla-Jensen  
 662 *Streptococcus acidi-lactici* Grot.  
 2371 *S. apis* Maassen  
 2701 *S. bovis* Orla-Jensen  
     *S. citrovorus.* See *Leuconostoc  
         citrivorum*  
 2702 *S. glycinaceus* Orla-Jensen  
 2705 *S. liquefaciens* Orla-Jensen  
     *S. paracitrovorus.* See *Leuconostoc  
         dextranicum*  
     *Streptothrix* Cohn. See *Actino-  
         myces*  
 1129 *Stysanus Stemonites* (Pers.) Corda  
 4097 *S. sp.*, R.C.  
 3155 *Syncephalastrum cinereum* Bain.  
 2699 *Tetracoccus casei* Orla-Jensen  
 2672 *Thamnidium chaetocladiooides*  
     Bref.  
 1127 *T. elegans* Link  
 3320 *Thielavia basicola* (B. & Br.) Zopf  
 1223 *Thielaviopsis ethaceticus* Went  
 1260 *T. paradoxo* (de Seynes) v. Höhn  
 3135 *Thiobacillus thiooxidans* Waks. &  
     Joffe  
     *Timothy grass bacillus.* See *My-  
         cobacterium Phlei*  
 2630 *Torula aclotina* Kufferath  
 2635 *T. aerius* Saito  
 2639 *T. alactosa* Kluyver  
 2638A *T. aurantiaca* Saito  
 2647 *T. aurea* Saito

4146 *T. botryoides* Brooks & Hansford  
 2052 *T. colliculosa* Hartmann  
 1134 *T. convoluta* Harz  
 2625 *T. corallina* Saito  
 1302 *T. cremoris* Hammer & Cordes  
 4481 *T. dattila* Kluyver  
 2626 *T. fermentati* Saito  
 2643 *T. flava* Saito  
 1746 *T. fuliginea* Berk.  
 2640 *T. galactosa* Kluyver  
 2648 *T. glutinis* (Cohn) Pringsheim &  
     Bilewsky  
 2634 *T. Gropengiesseri* Harrison  
 2636 *T. heveanensis* Groenwege  
     *T. histolytica.* See *Cryptococcus*  
 2645 *T. Holmii* Jörg.  
 2637 *T. lactosa* Kluyver  
 1847 *T. Laurentii* Kufferath  
 2646 *T. liposfera* den Dooren de Jong  
 2624 *T. lipolytica* Jacobsen  
 2623 *T. mineralis* Haydruck & Haehn  
 2644 *T. minuta* Saito  
 2622 *T. mucilaginosa* Jörg.  
 2632 *T. pulcherrima* Lindn.  
     820 *T. rosea*  
 2628 *T. rubescens* Saito  
 2627 *T. rubra* Saito  
 2649 *T. rubra* Schimon  
 2631 *T. rufula* Saito  
 2642A *T. rugosa* Saito  
 2629 *T. sanguinea* Schimon  
 1303 *T. sphaerica* Hammer & Cordes  
 3576 *T. utilis* Henn.  
     *T. spp.* from man. See *Crypto-  
         coccus*  
 2046 *Torulaspora fermentati* Saito  
 2051 *T. Roseii* Guill.  
 3153 *Torulopsis minuta* (Saito) Cif.  
     var. *parvissima* Cif. & Ashf.  
 3151 *T. nitritophila* Cif. & Ashf.  
 3369 *Trachysphaera fructigena* Tab. &  
     Bunt.  
 4418 *Trametes carnea* Nees & Fr.,  
     F.P.R.L.  
 4419 *T. gibbosa* (Pers.) Fr., F.P.R.L.  
 4420 *T. lilacino-gilva* (Berk.), F.P.R.L.  
 4421 *T. mollis* (Sommerf.) Fr., F.P.R.L.  
 4422 *T. odorata* Wulf., F.P.R.L.  
 4423 *T. pini* (Brot.) Fr., F.P.R.L.  
 4424 *T. protracta* Fr., F.P.R.L.  
 4425 *T. rubescens* (A. & S.) Fr.,  
     F.P.R.L.  
 4426 *T. serialis* Fr., F.P.R.L.  
 4427 *T. serpens* Fr., F.P.R.L.  
 4428 *T. suaveolens* (Linn.) Fr.  
 3076 *Trichoderma Koningi* Oudem.  
 3883 *T. lignorum* (Tode) Harz  
 4076 *T. sp.*, R.C.

4429 *Tricholoma rutilans* (Schaeff.) Fr., F.P.R.L.  
 2993 *Trichophyton album* Sabour. *T. acuminatum*. See *T. Sabouraudii*  
 3002 *T. asteroides* Sabour.  
 704 *T. balcanicum* Cast.  
 3000 *T. cerebriforme* Sabour.  
 2784 *T. decalvans* Cast.  
 3004 *T. depressum* MacCarthy  
 2995 *T. discoides* Sabour.  
 2992 *T. effractum* Sabour.  
 2996 *T. equinum* Matr. & Dassonv.  
 2997 *T. fumatum* Sabour.  
 2991 *T. glabrum* Sabour.  
 3003 *T. granulosum* Sabour.  
 3001 *T. lacticola* Sabour.  
 2786 *T. louisianicum* Cast.  
 2785 *T. nodoformans* Cast.  
 2994 *T. ochraceus* Sabour.  
 2998 *T. persicolor* Sabour.  
 2999 *T. plicatile* Sabour.  
 2521 *T. Sabouraudii* R. Blanchard  
 2522 *T. sulphureum* Fox  
 2520 *T. tonsurans* Malmsten  
 3367 *Trichosporium Pedrosoi* (Brumpton) Langer. (human pathogen)  
 3589 *Trichosporum Beigeli* Rabenh.  
*T. rugosum*. See *Hemispora Tyrothrix* Duclaux. See *Bacillus Unterhefe* I. See *Saccharomyces carlsbergensis*  
*Unterhefe* II. See *S. monacensis*  
 4073 *Ustilago Avenae* (Pers.) Jensen  
 3878 *U. Carbo* DC.  
 2211 *U. Zeae* Beck  
 4430 *Ustulina vulgaris* Fr., F.P.R.L.  
 4431 *U. zonata* (Schaeff.) Fr., F.P.R.L.  
 3387 *Venturia chlorospora* (Ces.) Karst.

2363 *V. inaequalis* Aderh.  
 1180 *V. pirina* Aderh.  
 2508 *Vermicularia Dematium* (Pers.) Fr.  
 2506 *V. Eryngii* Corda  
 2507 *V. trichella* Fr.  
 2512 *Verticillium albo-atrum* Reinke & Berth.  
*V. cinnabarinum*. See *Acrostalagmus*  
 4475 *V. ochro-rubrum* Desm.  
 2583 *Vibrio cuneata* Gray & Thorn.  
 2581 *V. cycloites* Gray & Thorn.  
 2582 *V. neocistes* Gray & Thorn.  
 1937 *V. percolans* Mudd & Warren  
 4432 *Volvaria bombycinia* (Schaeff.) Fr., F.P.R.L.  
 1670 *Wardomyces anomala* Brooks & Hansford  
 474 *Willia anomala* Hansen  
 1546 *W. belgica* Lindn.  
 3596 *W. margaretae* (Zender) Guill.  
 475 *W. Saturnus* Klöck.  
 4433 *Xylaria hypoxylon* (L.) Grev., F.P.R.L.  
 4434 *X. polymorpha* (Pers.) Grev., F.P.R.L.  
*Yeast* spp. See *Saccharomyces Zopfius* Wenner & Rettger. See *Bacterium*  
 813 *Zygosaccharomyces Barkeri* Sacc. & Syd.  
 2047 *Z. bisporus* Naganishi  
 2057 *Z. Nadsonii* Guill.  
 2058 *Z. Pastori* Guill.  
 4464 *Z. Priorianus* Klöck.  
 1813 *Z. sp.* from fig (Carlsberg Collection)  
 1814 *Z. sp.* from honey (Carlsberg Collection)

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A NEW SPECIES OF *GLOMERELLA* ON  
*CAMELLIA THEAE*

By A. C. TUNSTALL

(*Mycologist, Indian Tea Association*)

(With Plate XV and 1 Text-figure)

THE leaves of the tea plant are very commonly attacked by *Colletotrichum Camelliae*. The perfect form of this fungus—*Glomerella cingulata*—is also frequently present on the same leaves in north-east India. As a general rule the attacks of this fungus are confined to the leaves on which they cause a disease called brown blight. Occasionally it is found on the green internodes and less frequently on young red wood. During an investigation of the diseases of woody branches, a fungus was very frequently isolated from apparently sound wood in the vicinity of rotting lesions. This fungus was at first confused with *G. cingulata*, but further investigation showed that it was distinct. Although the form of the fructifications of both the *Colletotrichum* and the *Glomerella* type closely resembled that of *G. cingulata*, the dimensions were consistently larger. At first this was considered to be the effect of environment, but subsequent investigation showed that even when grown in the same environment for three generations the two fungi remained distinct. The new fungus was then given the name *Glomerella major*.

*Glomerella major* sp.nov.

*Mycelium* colourless at first, changing with age to very dark brown.  
*Colletotrichum* form:

*Conidia*, mean  $24.8 \times 7.7\mu$ , range  $14.4-30.6 \times 4.8-9.6\mu$ . 1-3 septate at germination; mostly cylindric with rounded ends, occasionally slightly curved; rarely attenuate at one end; finely granular contents; clear spot sometimes present at or near the middle.

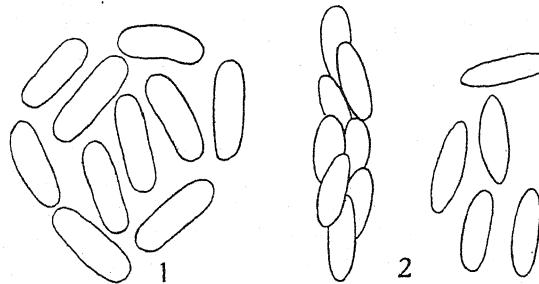
*Conidiophores* simple, or branched with brown walls; 2-3 septate; clavate; about double the length of the spores; apical enlarged cell  $6-8.5\mu$  in diameter. *Setae*  $100-200 \times 4.5-5\mu$ ; brown to opaque-brown; up to 4 septate; subacute, or uniform tint.

*Glomerella* form:

*Perithecia* very variable; diameter  $130-150\mu$ ; beaked ostioles commonly present with or without an apical tuft of brown hairs, sometimes spinose, dotted or warted; beaks, when present, cylindric or subconical, up to  $160 \times 100\mu$ . Opaque black walls up to  $50\mu$ ;

developed in a stroma beneath periderm, either remaining immersed or becoming erumpent with beaked ostiole.

Asci clearly defined only when immature; when mature about  $70-110 \times 10-18\mu$ ; paraphyses not present.



Text-fig. 1. *Glomerella major*. 1, conidiospores,  $\times 500$ ; 2, ascospores,  $\times 500$ .

Ascospores usually 8 in ascus; elliptic with obtuse or subacute tips; frequently slightly inequilateral; not allantoid; clear spot at the middle; mean  $24.9 \times 7\mu$ , range  $15.6-30.1 \times 5.5-8.4\mu$ ; walls usually become brown when released into perithecial cavity; germination sometimes occurs in the cavity, the spores becoming 1-2 septate, rarely 3 septate.\*

COMPARISON WITH *GLOMERELLA CINGULATA* (STONEM.)  
SPAULD. & VON SCHR.

Apart from the dimensions the above description may apply to *G. cingulata*. It is therefore very important to determine the size of the spores with accuracy.

\**Glomerella major* sp.nov.

Mycelium primum hyalinum, deinde senectute valde fuscum.  
forma *Colletotrichoides*:

Conidiis circa  $24.8 \times 7.7\mu$  (variantibus  $14.4-30.6 \times 4.8-9.6\mu$ ), 1-3 septatis, plerumque cylindricis utrinque rotundatis, subinde curvulis, raro ad apicem unum attenuatis; intus minute granulosis, in medio guttula hyalinâ aliquando praebitis.

Conidiophoris simplicibus ramosis fuscis, 2-3-septatis, clavatis, quam sporis bis longioribus; cellulâ dilatata apicali  $6-8.5\mu$  diam.; setis  $100-200 \times 4.5-5\mu$  fuscis vel opaco-fuscis, usque ad quater septatis, subacutis, unicoloribus.

forma *Glomerelloides*:

Peritheciis maxime varieformibus,  $190-150\mu$  diam., plerumque osteola rostrata saepe fasciculo pilorum fuscorum ornata, tum spinosa, tum punctata sive verrucosa, gerentibus; nostris cylindricis subconicis, usque ad  $160 \times 100\mu$ ; peritheciis integumento opaco nigro usque ad  $50\mu$ , in stromate infra periderma evoluto, aut semper immerso aut erumpente et osteolum rostratum gerente.

Asci solum in immaturitate distinctis, in maturitate c.  $70-110 \times 10-18\mu$ , paraphysibus nullis; ascosporis plerumque octonis, ellipticis, obtusis subacutis, saepe aliquanto inequilateralibus haud allantoides; in mediis guttula hyalina praebitis, c.  $24.9 \times 7\mu$  (variantibus  $15.6-30.1 \times 5.5-8.4\mu$ ), ad maturitatem fuscis; nonnunquam intra peritheciis cavitatem germinantibus, 1-2 raro 3 septa evolventibus.

For this purpose material was obtained from eight different sources embracing all the tea areas in north-east India. Of each type not less than a hundred spores taken at random were measured. The results are shown in microns in the following table.

	Length		Breadth	
	Arithmetic mean	Standard error	Arithmetic mean	Standard error
Ascospores:				
<i>G. major</i>	24.9	0.18	7.0	0.05
<i>G. cingulata</i>	14.4	0.16	4.4	0.08
Difference	10.5	± 0.24	2.6	± 0.99
Conidiospores:				
<i>G. major</i>	24.8	0.19	7.7	0.04
<i>G. cingulata</i>	15.4	0.18	4.7	0.04
Difference	9.4	± 0.26	3.0	± 0.05

It is clear from the above that the differences in dimensions are significant.

There are other differences which are not so definite. *G. major* has a more marked tendency, especially in culture, to produce long beaks on the perithecia. Both fungi produce hairs round the beaks of the perithecia when grown in very humid conditions but *Glomerella major* tends to produce relatively longer hairs.

The setae on the *Colletotrichum* form of both fungi are more numerous, and longer, under humid conditions. In *Glomerella cingulata*, setae were sometimes absent from the conidial accervuli but pure cultures made from them developed setae.

It is probable that the development of setae on the accervuli and hairs on the perithecia in both *G. cingulata* and *G. major* are influenced considerably by the atmospheric conditions; the development of the beak on the perithecia may be influenced similarly. As these characters are variable, the dimensions recorded should be accepted with caution.

The emergence of the perithecia of *G. major* from the substrata is also influenced by conditions of growth. In the field, the perithecia tend to remain immersed in the bark, while in a damp chamber it is not uncommon to find them growing freely on the surface.

It has been observed that hyaline ascospores squeezed out of a perithecium will germinate readily in water, producing not more than one septum, and without darkening in colour. On the host tissue however, the spores become darker and frequently form more than one septum when germinating. *G. cingulata* behaves similarly.

Both conidia and ascospores produce appressoria, which in culture on corn meal agar may be formed in long chains. In the field the appressoria are generally isolated, rarely two or three together. Once, however, masses of chains similar to those produced in culture were

observed on tea branches in the field. *G. cingulata* has not been seen to produce chains of appressoria even in culture.

Both the conidial and the perithecial forms have been produced from single spore cultures of either form and there is no evidence of heterothallism. *G. cingulata* does not form perithecia readily from single spore cultures.

#### THE OCCURRENCE OF *GLOMERELLA MAJOR*

Specimens of branches which had failed to produce new growth after pruning were selected at random from a number of plots situated on a tea garden in the Dooars. They were each divided into two portions, separating the one-year from the two-year-old wood. The portions were flamed and placed in separate sterile tubes with a little sterile water. In most of the branches the one-year-old wood was dead, while the two-year-old wood was alive at the time of collection. The collection was made from three series each containing six plots, and was continued for forty weeks. The tubes were examined from time to time during a period of four months subsequently.

More than thirty distinct organisms were found on the branches examined. Apart from the common moulds, such as *Penicillium*, *Glomerella major* was the most common fungus present on both the living and dead portions of the twigs. *G. cingulata* was not found. *G. major* appears to be able to attack both dead and living tissues with equal facility. The infection was evidently greater in the latter part of the season.

The following table summarises the observations made.

#### *Glomerella major*

Periods of five weeks commencing March 7th	Stems bearing either or both forms			Percentage of total infected portions bearing	
	Top portion max. = 90	Bottom portion max. = 90	Total max. = 180	Perithecial form	Conidial form
March-April	38	30	68	83	45
April-May	19	20	39	64	53
May-June	29	35	64	57	57
June-July	33	30	63	19	98
July-Aug.	31	32	63	11	98
Aug.-Sept.	48	63	111	43	94
Oct.	49	48	97	81	87
Nov.	50	51	101	98	47

The occurrence of the two forms showed marked differences at different periods of the year. The conidiospores were produced most frequently on stems collected in the rainy season, while the perithecial form was markedly less at this season. It is interesting to note that the conidiospores have sticky coats and are thus readily distributed by insects, etc., while the ascospores are more suitable for distribution by

the wind. It is suggestive that the sticky spores are produced most freely at the time of the year when insects are most prevalent. The behaviour of *G. cingulata*, the Brown Blight fungus, is very similar in this respect.

At the end of the period during which the observations were made, ten apparently healthy branches were taken from each of the plots when pruning, two branches from each group of tea being taken at random and in two portions. One portion was taken immediately above the pruning cut, *i.e.* to one-year-old wood and the other from the green stems immediately above the wood. The stems were flamed and placed in sterile tubes as before and examined three months later. In these branches the bottom portions corresponded to the top portion of the moribund ones (see preceding table), none of which bore any green wood. In the following table the moribund twigs received during the five weeks preceding the collection of the healthy ones are compared with the latter.

*Percentage of tubes infected*

Description	<i>G. major</i>	<i>G. cingulata</i>
Moribund twigs. Top portion	56	0
Apparently healthy prunings. Bottom portion (corresponding to top portion of moribund twigs)	10	0
Green portion (not present on moribund twigs)	20	13

It would appear that *G. major* is able to attack both woody and green tissues, while *G. cingulata* seems to be confined to the green tissues.

It is interesting that apparently healthy prunings, from plots which had been sprayed twice with lime sulphur solution, produced no *G. major* on their green portions, while the spraying appeared to have had no effect at all in lessening the percentage of infection on the woody portions. It seemed possible that the infection of the green portions was mostly superficial so that they were exposed to the action of the fungicide while the fungus was within the tissues of the woody portions. This supposition was confirmed by microscopic examination.

**THE ASSOCIATION OF *GLOMERELLA MAJOR* WITH DISEASE**

The dying back of branches after pruning is not necessarily due to the presence of parasitic organisms. Dry winds and lack of reserves in the plant have been found to exercise a marked influence. If, however, a dead branch is allowed to remain on the plant it frequently starts a rotting hole. The actual rotting is usually associated with the presence of Basidiomycetes, such as *Poria hypobrunnea*. In the microscopic examination of the specimens mentioned above—more than

1500—no mycelium resembling that of a Basidiomycete was observed.

In another experiment, bearing on the treatment of pruning cuts, 240 large cuts were examined microscopically, as well as in culture, one year after they were made, and no Basidiomycetes were found. It was not until the second year after cutting that fungi of that group were detected.

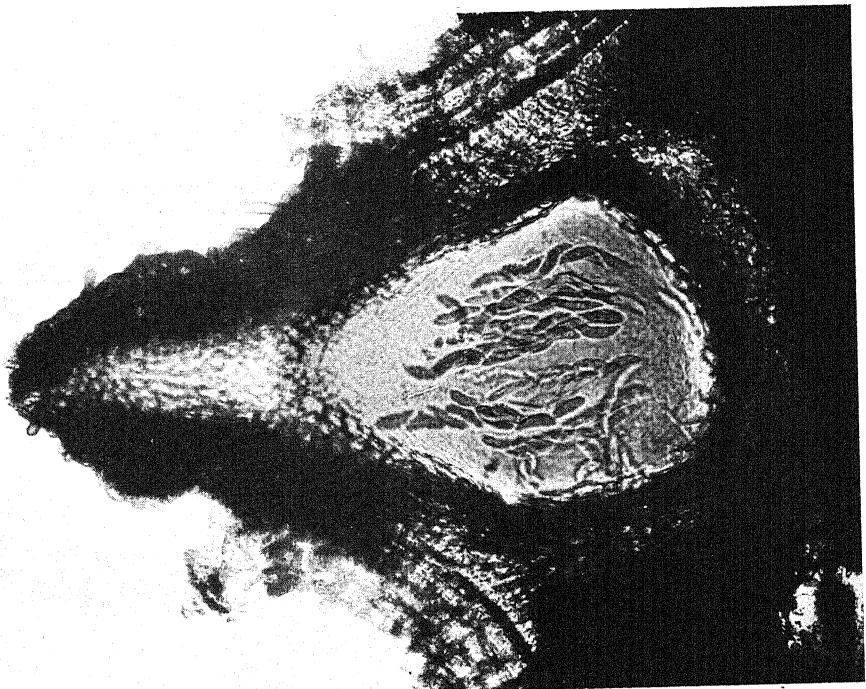
On the other hand large numbers of rotting snags have been examined from all the tea districts in north-east India, and almost invariably it has been found possible to isolate *Glomerella major* from the apparently sound tissues adjacent to the rotting ones. No other fungus has been found so consistently.

As the parasite is present frequently in apparently healthy branches it is evident that vigorous plants exhibit a considerable degree of resistance to injury from its attack. *G. cingulata* seems to behave similarly. The latter fungus may be found on most tea bushes in north-east India but it causes noticeable injury only to tea plants weakened by other causes.

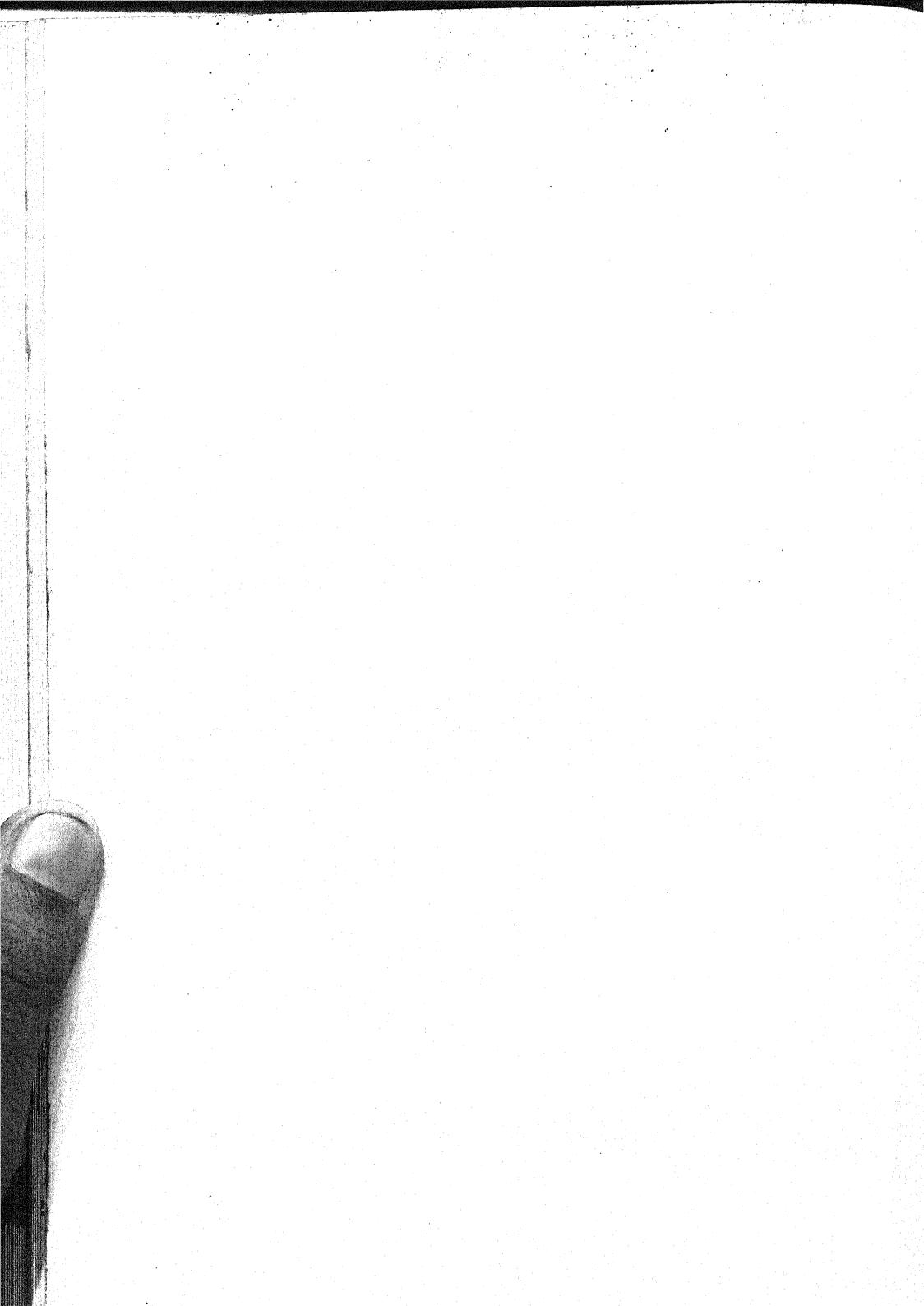
The writer wishes to acknowledge with many thanks the help of the Imperial Mycological Institute in examining and reporting on slides and specimens in connection with this investigation. He desires also to thank Mr E. W. Mason for drawings of the conidiospores and ascospores from the slides.



A perithecium of *Glomerella cingulata* on tea leaf reproduced on the same scale as that of *G. major* to show difference in size.



A perithecium of *Glomerella major* on tea stem.



THE PRESENCE AND ABSENCE OF AN ENDO-  
PHYTIC FUNGUS IN *LOLIUM TEMULENTUM*  
AND *L. PERENNE*

By KATHLEEN SAMPSON, M.Sc.  
(*University College of Wales, Aberystwyth*)

I. INTRODUCTION

INTEREST in the endophytic fungus of *Lolium* dates back to 1898 when Vogl recorded mycelium in the seed of *L. temulentum*. This was confirmed in the same year by Guérin(4), Hanausek(5) and Nestler(10), and in 1902 Neubauer and Remer added *L. remotum* to the list of species infected. Poisonous properties were already attributed to Darnel, and the idea that its toxicity might be linked with the fungus invading the seed added to the interest in its discovery, but such a connection has never yet been substantiated.

The best description of the progress of mycelium in the young ovule, the fruit and the embryo, is that of Freeman(3). He worked for the most part with *L. temulentum* and incidentally expressed his belief in the existence of strains lacking the fungus which could, he thought, be distinguished from infected grains by colour, but the possibility that the samples contained mixed types of the grass was not considered in this connection.

Hannig(6), who followed the transmission of the fungus through four generations of *L. temulentum*, found that fungus-free lines grown in open ground suffered no new infection, while invaded plants usually gave infected seed. Rarely a single grain in the infected series might miss the mycelium and form the starting point for a fungus-free population. Hannig states that in his cultures fungus-free fruits could be recognised only by microscopic examination.

Miss McLennan(8) made a detailed study of the invasion of *L. perenne*, and came to the conclusion that all plants of this species carry the endophytic fungus. She also differed from all previous authors in finding intracellular mycelium, but a careful study of her figures throws some doubt on this point.

A second paper by the same author(9) dealt with a fungus invading the roots of *L. perenne*. The organism described possesses non-septate intracellular mycelium with the sporangioles, vesicles, and more rarely arbuscles, characteristic of mycelia recorded in the roots of higher plants by other authors(12, 13, 16, 17). McLennan admits the absence of proof regarding the identity of this fungus with that found in the seed of *Lolium* sp., but the unfortunate title of the second paper

and a parallel drawn between the invasion of the grass and that of *Calluna vulgaris* by *Phoma radicis*(14) has led subsequent writers to accept the view that *L. perenne* is invariably associated with a Phycomycete which invades both the root and the shoot systems, and is transmitted by the seed(1, 2). Since a preliminary examination failed to substantiate this, experiments were initiated with the object of collecting further data on the relationship between *Lolium* spp. and the fungus often found in their fruits.

## II. FREE AND INFECTED POPULATIONS OF *L. TEMULENTUM*

In 1929, with the kind assistance of Mr F. G. Preston, Superintendent of the Cambridge Botanic Garden, twenty packets of seed of *L. temulentum* were obtained from different Botanic Gardens in Europe. Microscopic examination of several fruits from each packet indicated that the samples could be classified on the presence or absence of mycelium as positive, negative or mixed. The number of samples containing infected fruits was larger than the number recorded as negative, indicating, as previous reports suggest, that the fungus-infected races of Darnel are widely distributed. These samples, sown in 1929 and 1930, formed the starting point of lines upon which the following observations were made.

At an early stage in the work an attempt was made to trace the mycelium back from the ovary to the base of the floral axis. This proved to be an unexpectedly easy task, since the mycelium is very abundant in the pith and persists there until maturity. It can be found without much difficulty even in fragments of pith taken from dry stems after harvest. To scrape the pith from a flowering stem, stain with cotton blue and examine under the microscope occupies from five to seven minutes, and this method has been used extensively in recording the presence and absence of mycelium in the populations of plants kept under observation. The results obtained have been confirmed from time to time by microtomed preparations of ovaries at different stages of growth and by hand sections of mature seed. The staining methods used were those described in a paper dealing with *Epichloe typhina*(15). The most complete series of observations was made on eight lines, the parents of which were selected and classified in 1929. Of these, three carried the fungus and four were fungus-free.\* The general procedure was to grow each season in open ground ten plants of each line and to examine, by the pith-scraping method, at least two spikes from each plant. The total number of stems examined in this experiment is given in Table I where the records made on separate lines have been pooled in each of the two series.

\* The term "fungus-free" is used throughout the paper only to denote the absence of that type of septate mycelium which permeates the vegetative organs, forms a zone outside the aleurone layer and is transmitted by the seed.

Table I. *Presence and absence of mycelium in the flowering stems of Lolium temulentum grown for four generations as single plants*

Year	Fungus present in 3 selected parents, 1929		Fungus absent in 5 selected parents, 1929	
	Mycelium in flowering stems	Present	Mycelium in flowering stems	Absent
1930	66	17	1?	90
1931	31	1	0	23
1932	26	0	2?	85
1933	24	0	0	45
Totals	147	18	3?	243

In the populations derived from infected parents, only eighteen out of 147 stems were recorded as negative. The probability is that the mycelium was either missed in removing the pith or overlooked by the observer, since seed from the plants thus recorded as negative showed characteristic mycelium in abundance.\* In these experiments with Darnel I have found so far no example of a fungus-free plant originating from an infected parent. Such cases might reasonably be expected to occur at times and some were actually recorded in Hannig's cultures of *L. temulentum* (6) and in my own populations of *L. perenne* (p. 341).

In the families derived from five parents selected in 1929 as fungus-free, 243 stems were examined and three were recorded as containing mycelium. It is believed that the mycelium in these three stems belonged to another fungus, possibly *Helminthosporium* sp. since traces of stripe disease appeared on some of the plants. Certainly the seed derived from the plants thus recorded as positive showed no signs of mycelium and their descendants were likewise fungus-free. In so far as the *Lolium* endophyte is concerned, the infected and non-infected lines remained true for this character through five generations.

### III. CROSSES BETWEEN FREE AND INFECTED PLANTS OF *L. TEMULENTUM*

In the experiment just described the plants were grown in the open ground with no control of pollination. Since *L. temulentum* is highly self-fertile the probability is that self-pollination occurred almost exclusively. Microscopic observations on the distribution of the fungus in infected plants suggests that the fungus is normally carried only via the ovule. In confirmation of this, and in order to obtain additional evidence for the existence of fungus-free plants, reciprocal crosses were made between parent plants selected from the above experi-

\* Another possibility is that a single inflorescence may sometimes miss infection. This could not be proved, as the seed examined was of necessity taken from another spike on the same plant.

ments. The technique of crossing was carried out entirely by Mr A. R. Beddows, M.Sc., whose help I gratefully acknowledge. Data collected from the first, second and third generations are summarised in Table II. The crosses were made in 1931 under carefully controlled conditions in a greenhouse, while  $F_2$  and  $F_3$  generations resulted from the natural self-pollination of  $F_1$  and  $F_2$  plants grown in the open.

Table II. *Crosses between free (553) and infected (547) plants of L. temulentum*

Year	Parents	Cross. Female parent is first named	Generation No.	Seed	Plants
1931	547+	—	—	—	—
	553—	—	—	—	—
1932	547+(20)*	553×547	$F_1$	—(5)	— (16)
	553—(26)	547×553	$F_1$	+(5)	+ (21)
1933	547+(10)	553×547	$F_2$	—(5)	— (112)
	553—(10)	547×553	$F_2$	+(5)	+ (95)
1934	547+(5)	553×547	$F_3$	—	— (5)
	553—(5)	547×553	$F_3$	—	+ (10)

\* Figures in brackets refer to the number of observations made. The results were consistent throughout the experiment. A plus sign (+) indicates the presence of mycelium; a minus sign (—) indicates its absence.

The fungus-free parent (553) is one which has now remained free from infection through six generations (1929-34), while parent 547 has been consistently infected over the same period. In reciprocal crosses only those seeds and plants were infected which had 547 as the female parent.  $F_2$  and  $F_3$  generations were consistently either infected or fungus-free, according to which parent plant functioned as the female in the original cross.

The two parents selected differed also somewhat markedly in certain vegetative characters, 553 being a multi-tillering leafy type, while 547 had rather few strongly developed stems. Observations on the segregates of each cross showed that the characteristics of the parent were in no way connected with the presence and absence of the fungus. It has been possible to select from the  $F_3$  generation of cross 553×547 a plant which had the habit of 547 but lacked the fungus; in family 547×553 plants occurred which closely resembled 553, but were infected. Such results indicate the danger of making a comparison between infected and non-infected plants of *Lolium* sp. without recognition of their possible origin from different strains of the host species. The statement by Freeman (3) that infected plants of Darnel are more vigorous and more productive, and the result of Hannig (7) that they contain more nitrogen than fungus-free races, are possibly subject to this error.† Until we have obtained, by inocula-

† In a footnote to the fourth edition of his *Pflanzenphysiologie* Jost states that Hannig expressed verbally his doubt about nitrogen fixation by the *Lolium* endophyte.

## Endophytic Fungus in *L. temulentum* and *L. perenne* 341

tion, infected and non-infected individuals of the same strain of the host plant a comparison may be made using  $F_1$  plants obtained from a reciprocal cross between an infected and a non-infected plant. The crosses discussed here were made with this object in view, and detailed observations and measurements have been made on single  $F_1$  plants. The results will be presented when data are available from a second experiment dealing in a similar manner with *L. perenne*. Concerning *L. temulentum* the available facts indicate that the effect of the fungus on its host, whether for good or ill, is too small to be discernible either by eye observation or by any method of measurement adopted by me.

### IV. FREE AND INFECTED POPULATIONS OF *L. PERENNE*

In 1929 a preliminary examination of wild and pedigree plants of *L. perenne* led me to conclude that an endophytic fungus is by no means universally present in this species. Three plants were finally selected for generation studies which have been carried on for six years. The details of procedure were essentially the same as for *L. temulentum*, except that the perennial character of the host made it possible to include observations on the over-wintering of mycelium in the tiller buds and its distribution in propagants.

In one of the selected parents the mycelium present stained only faintly with cotton blue, and it was distinctly less easy to detect in pith scrapings and in sections. After growing populations of this strain of the grass for several generations evidence appeared showing that it carried a fungus other than that usually indicated by the term *Lolium* endophyte. The details of this type of infection will be given in a future paper. Of the remaining plants one was fungus-free and the other carried what I believe to be the typical endophyte similar to that in *L. temulentum*. The data obtained are given in Table III.

Table III. Free and infected populations of *L. perenne*

Year	Parent (1975) selected as fungus-free 1929		Parent (1971) selected as infected 1929	
	Mycelium in flowering stem		Mycelium in flowering stem	
Present	Absent	Present	Absent	
1931 progeny*	0	21*	26*	2*
1932 progeny	0	22	55	1
1932 propagants	0	20	20	0
1933 progeny	0	40	36	11†
1934 progeny	0	20	20	10†
1934 propagants	0	6	6	6†

\* The figures for 1931 include a few observations made in 1930. In this year very few spikes were produced by the seedling plants. This difficulty was overcome in subsequent years by sowing soon after harvest.

† These figures include the progeny of a plant which missed infection in 1932. Data for every individual plant were always kept separate, but they are pooled in this table.

The behaviour of the plant-populations derived from the fungus-free parent (1975) can be dismissed briefly. No new infection occurred, both the progeny and the propagants remaining consistently free from invasion by the *Lolium* fungus. All the progeny examined from the infected plant (1971) carried the fungus in 1931-32, but in 1933 a single individual was noticed as having apparently escaped infection from its parent. The absence of the fungus was confirmed in both the progeny and the propagants of this plant in 1934 (Table III).

These experiments confirm the suspected existence of fungus-free races of *L. perenne* and indicate that they may arise from infected plants. We have as yet no knowledge as to how or when members of the genus *Lolium* became invaded by this fungus.

#### V. CROSSES BETWEEN FREE AND INFECTED PLANTS OF *L. PERENNE*

The families of plants discussed in the preceding section were derived from spaced plants in garden soil with no control of pollination. Since *L. perenne* is a cross-pollinated species it is almost implicit in the results (Table III) that only the female organ carries the fungus. Confirmation of this was, however, obtained from certain hybrids and their parents which Dr T. J. Jenkin kindly allowed me to examine from the cultures of plants prepared for his genetical studies (Table IV).

Table IV. *Crosses between free and infected plants of L. perenne and L. italicum*

Ref. to	Mycelium in $F_1$	Female parent	Mycelium	Male parent	Mycelium
1065	Absent	<i>L. italicum</i>	Absent	<i>L. perenne</i>	Present
1063	Present	<i>L. perenne</i>	Present	<i>L. perenne</i>	Absent
1159	Absent	<i>L. perenne</i>	Absent	<i>L. perenne</i>	Present

#### VI. SUMMARY

The study of a series of pedigree populations of single plants of *L. temulentum* and *L. perenne* extending through six seasons has shown that both species can exist either with or without an endophytic fungus.

This fungus, when it occurs, invades the leaves, stems and tiller buds, and in a perennial plant it is distributed by vegetative propagation. It does not appear to invade the roots and it is in my opinion distinct from the Phycomycete type which has been recorded in these and other grasses, and in plants not closely related.

The *Lolium* endophyte invades the ovule, and that it is mechanically inherited from the female parent only has been shown by the reciprocal crossing of free and infected plants.

## *Endophytic Fungus in L. temulentum and L. perenne* 343

While races free from infection may arise from infected individuals, the origin of the infected races themselves is still obscure.

The problems of chief interest, namely, the identity of the organism and the biological aspects of its connection with the grasses, still await solution. That the relation is not an obligate one so far as the higher plant is concerned emerges from the experimental work discussed in this paper.

### ACKNOWLEDGMENTS

I am indebted to Mr E. L. Hughes, M.Sc., and to Mr P. T. Thomas, B.Sc., who gave valuable help as student assistants during several summer vacations, and to Mr J. W. Watkins for his careful supervision of cultural details.

I wish to thank most cordially Prof. R. G. Stapledon, C.B.E., M.A., for granting me full use of the facilities of the Welsh Plant Breeding Station.

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## PROCEEDINGS

Meeting held at University College, London, November 17, 1934,  
Dr B. BARNES, President, in the Chair.

W. M. WARE. Mushroom growing in the United States of America.

The cultivation of mushrooms is a great and specialised industry in the U.S.A.; it has been brought to a high state of perfection by the growers themselves and is assisted by some half-dozen scientists who are carrying out research and advisory work in the mycological, entomological and chemical problems connected with it.

During the month of May 1934, with a Travelling Fellowship granted by the Ministry of Agriculture and Fisheries, a visit was paid to some of the Eastern States of the U.S.A. and it was possible not only to see numerous growing "plants" (the largest of which has one million sq. ft. of bed surface) but also to confer with research workers.

As a result of the experience gained, it is possible to appreciate the differences between American and English methods. The most noticeable is that, with few exceptions, the American growers construct specially designed buildings of standard type and, by the adoption of the tier system, they make the fullest use of the space available. This method of growing mushrooms also provides the best opportunity for making fumigation effective. Of the 516 growers included in the Horticultural Census, 363 are to be found in the State of Pennsylvania. The cropping period is limited to winter and spring because, although cooling systems are sometimes installed, they are not capable of counteracting completely the very high temperatures from May to September. Stable manure is still used for making the compost for the beds; substitutes are being sought and some have given hopeful results but at the present time the growers are not advised to abandon the natural for the more artificial medium. Storage of manure for several months, in very large and much compressed piles, is a practice adopted in Pennsylvania and one which is not seen in England.

Canneries, devoted entirely to the mushroom crop, are attached to some growers' premises; they are each capable of dealing with from three and a half to six tons of mushrooms a day.

Pure-culture spawn of high quality is made by about a dozen of the larger growers and a great quantity is exported to England. The process of manufacture is a commercial secret, but it is possible to see that the laboratories and equipment are well designed and scrupulously clean.

Co-operation is exemplified by a Mushroom Growers' Association with a membership of over 300. The M.G.A. buildings are situated at Kennett Square, Pa., and though they are primarily for commercial purposes, it is noteworthy that they include laboratory accommodation and an experimental mushroom house.

The fungus diseases of the crop are the same as those met with in England but American mushroom beds are not invaded by *Xylaria vaporaria* or *Clitocybe dealbata*. A truffle, *Pseudobalsamia microspora*, not yet recorded in England, is causing apprehension not only on account of its invasion of mushroom beds but also because of its persistence for several years in houses where it has once obtained a footing.

D. M. CAYLEY. Field Observations on, and Cultural Experiments with, Wild and Cultivated Forms of Edible Mushroom.

Examination of a number of grass roots from sods which had carried pilei of *Psalliota campestris* and *P. arvensis* showed that the roots of many different species of

grass are very generally infected with several different types of mycelia, one of which is believed to be *Psallioita*.

Artificial infections under sterile conditions of four different species of grass seedlings have shown that the two wild species, *P. campestris* and *P. arvensis*, can penetrate and live in the roots for some months without materially affecting the growth of the grass. Positive artificial infections of the same species of grass have also been obtained with the white and fuscous forms of cultivated mushrooms, provisionally called *P. hortensis*. The type of mycelial growth in the cells of the artificially infected host plant closely resembles that found in certain types of natural infection.

Both *P. campestris* and *P. arvensis* can form "fairy rings" on pastures. With *P. campestris*, the grass on the ring appears to benefit in some way by the presence of the fungus, the grass being a darker green and of more luxuriant growth. With *P. arvensis*, on the other hand, the growth of the grass is poor.

The spores of *P. campestris* will germinate in Knop solution, without previous treatment, in from ten to twenty-one days, but success mainly depends upon the condition of the pileus when the spore trace is taken. Successive spore traces from the same pileus, taken at intervals of from twelve to twenty-four hours, have shown that the first shed spores from an immature pileus do not germinate under artificial conditions. The best germination is obtained from fully expanded pilei when the gills are umber in colour. With due precautions, the spore traces from fully expanded clean pilei were found to be mostly free from contamination. Kept under dry conditions, the spores of *P. campestris* remain viable for about six months, those of *P. hortensis* rather longer. Attempts to germinate the spores of *P. arvensis* in Knop solution have failed, partly owing to lack of mature spores.

#### W. J. DOWSON. The Occurrence of *Aplanobacter Rathayi* in Britain.

There are three similar bacterial diseases of cereals and grasses in which the conspicuous symptom is the malformation of the inflorescence and the presence on it of a copious yellow bacterial slime. *Aplanobacter Rathayi* is known only in Europe and attacks *Dactylis glomerata*; *Aplanobacter Agropyri* occurs in the Western United States on *Agropyron Smithii*, and *Bacterium Tritici* is found on wheat in conjunction with eelworm, *Tylenchus tritici*, from Cyprus to Western Australia. Until recently *Aplanobacter Rathayi* had not been recorded definitely for Britain although suspected in Wales and Scotland; but in the summer of 1934 a large patch of Cocksfoot grass was found heavily infected on the bank of the river Cam, not far from Cambridge. When inoculated directly into young plants typical symptoms resulted; but pure cultures of the yellow organism failed to produce inoculation. In isolating this organism by the plate method two other bacteria were also found in the naturally occurring slime: one, a white gram positive form, the other a gram negative organism. E. F. Smith found much the same thing, as did also O'Gara with *A. Agropyri*, and the question arises as to which of the three organisms is the real parasite, in view of the fact that the gram positive yellow one in pure culture fails to produce infection. Possibly a combination of all three, or of any two, is necessary to bring about the typical symptoms of the disease. In the three diseases mentioned, at least two organisms are constantly and intimately associated, viz. a white, motile gram positive bacterium with the two species of *Aplanobacter*, and the eelworm, *Tylenchus tritici* with *Bacterium Tritici*.

#### A. R. WILSON. Observations on the Occurrence of Bacterial Plant Diseases in the United States.

A comparison was made of the status of bacterial plant pathology in Great Britain and the United States. A brief account was then given of several bacterial diseases observed during the summer of 1934 in various parts of the United States, including a brief review of the Crown-Gall situation in that country. In conclusion

an account was given of a survey of the incidence of Fire Blight of apples in the State of Wisconsin, including a discussion of the influence of climatic factors on the occurrence of the disease, and the possible influence of these factors on an outbreak of the disease in Great Britain. A brief description was given of the methods adopted for the control of Fire Blight at the University Field Station at Gays Mills, Wisconsin.

MRS M. D'OLIVEIRA. Notes on *Bacterium Savastanoi*.

*Bacterium Savastanoi* and its variety *Fraxini* cause respectively the diseases known as olive knot and ash canker, the former occurring wherever the olive is grown; the latter only in Europe. Comparisons have been made hitherto in the United States by E. F. and C. O. Smith. The present account deals with similar work carried out at the Botany School, Cambridge. By numerous infection experiments on a range of hosts it was shown that (1) in this range of hosts there was none which could be infected by both organisms and (2) that the olive knot organism, *B. Savastanoi*, always produces knots or overgrowths as a result of infection, whereas the ash parasite, *B. Savastanoi* var. *Fraxini* always forms a canker-like lesion. Culturally, both organisms are similar, as E. F. Smith demonstrated: but in view of the different and constant pathological effects the designation of the ash organism as a variety only of the olive bacterium should be reconsidered. In south England the ash bacterial disease is often complicated by the presence of *Nectria* which alone or together with the bacterium produces an overgrowth.

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185. Kent, Mr G. C., Botany Department, Iowa State College, Ames, Iowa, U.S.A. (1932.)
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200. McDonald, Mr J., D.F.C., B.Sc., F.L.S., Mycologist, Department of Agriculture, Box 323, Nairobi, Kenya Colony, East Africa. (1923.)
201. Macdonald, Mr J., 25, Drumsheugh Gardens, Edinburgh. (1929.)
202. McFarland, Dr Frank T., Department of Botany, University of Kentucky, Lexington, Ky., U.S.A. (1924.)
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209. Mason, Mr E. W., M.A., M.Sc., F.L.S., Imperial Bureau of Mycology, 17, Kew Green, Kew, Surrey. (1921.)
210. Mason, Mrs E. W., Inglenook, 63, King's Road, Richmond, Surrey. (1922.)
211. Mason, Mr F. A., F.R.M.S., M.S.P.A., 29, Frankland Terrace, Leeds. (1912.)
212. Matthews, Professor J. R., M.A., F.L.S., Department of Botany, The University, Old Aberdeen. (1921.)
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221. Miyabe, Dr Kingo, Professor Emeritus of Botany, Hokkaido Imperial University, Sapporo, Japan. (1919.)

222. Montague, Mrs A., Penton, Crediton, N. Devon. (1898.)  
223. Montana Experiment Station, Department of Botany and Bacteriology, Bozeman, Montana, U.S.A. (1930.)  
224. Montreal, Canada, Faculté des Sciences, Institut Botanique, Université de Montréal. (1932.)  
225. Moore, Mr W. C., M.A., Ministry of Agriculture, Pathological Laboratory, Milton Road, Harpenden, Herts. (1922.)  
226. Morgan, Dr G., Ashley-Hatton, Dyke Road Avenue, Brighton. (1928.)  
227. Morris, Mr L. E., 15, Tenison Avenue, Cambridge. (1924.)  
228. Muller, Dr H. R. A., Institut voor Plantenziekten, Buitenzorg, Java. (1932.)  
229. Murphy, Professor P. A., Sc.D., A.R.C.Sc.I., M.R.I.A., Department of Plant Pathology, Albert Agricultural College, Glasnevin, Dublin, N.W. 3. (1924.)  
230. Murray, Mr G. H., F.E.S., Director of Agriculture, Rabaul, New Britain, Territory of New Guinea, *via* Australia. (1921.)  
231. Muskett, Mr A. E., M.Sc., A.R.C.S., Queen's University, Belfast, Northern Ireland. (1923.)  
232. Nannfeldt, Dr J. A., Sturegatan 11, Uppsala, Sweden. (1932.)  
233. National Collection of Type Cultures, Curator, Lister Institute, Chelsea Gardens, London, S.W. 1. (1921.)  
234. National Museum of Wales, Cardiff. (1924.)  
235. Nattrass, Mr R. M., B.Sc. (Agric.), Ph.D., Department of Agriculture, Nicosia, Cyprus. (1925.)  
236. Nebraska, The Library, University of, Lincoln, Nebr., U.S.A. (1924.)  
237. Nederlandsche Mycologische Vereeniging, c/o Mr A. C. S. Schweers, Nassaulaan 17, Alkmaar, Holland. (1920.)  
238. Nelson, Miss M. G., M.A., Botanical Department, The University, Oxford. (1932.)  
239. New York Botanical Garden, Bronx Park, New York, U.S.A. (1904.)  
240. Nicholson, Mr W. E., F.L.S., 50, St Anne's Crescent, Lewes. (1913.)  
241. Noel, Miss E. F., F.L.S., 37, Burnham Court, Queen's Road, London, W. 2. (1913.)  
242. Norman, Mr L. Stafford, Konjeni Estate, Luchenza P.O., Nyasaland. (1927.)  
243. North Carolina, Library, University of, Chapel Hill, North Carolina, U.S.A. (1920.)  
244. Nursery and Market Garden Industries' Development Society, Ltd., Experimental and Research Station, Cheshunt, Herts. (1922.)

245. Oberlin College, Oberlin, Ohio, U.S.A., Library, Department of Botany. (1933.)
246. O'Connor, Mr P., Ph.D., B.Sc., A.R.C.Sc.I., National Museum, Dublin. (1925.)
247. Ogilvie, Mr L., M.A., M.Sc., Research Station, Long Ashton, nr Bristol. (1922.)
248. Oke, Mr Alfred William, B.A., F.G.S., F.L.S., 32, Denmark Road, Hove, Sussex. (1908.)
249. Ontario Agricultural College, Library, Guelph, Ontario, Canada. (1920.)
250. Osborn, Professor T. G. B., D.Sc., F.L.S., Botanical Department, The University, Sydney, N.S.W., Australia. (1910.)
251. Ottawa, Ontario, Canada, The Library, Geological Survey. (1926.)
252. Overholts, Dr L. O., Botany Department, Pennsylvania State College, Pa., U.S.A. (1929.)
253. Page, Miss W. M., M.Sc., 19, Ledam Buildings, Bourne Estate, Holborn, London, E.C. 1. (1921.)
254. Park, Mr M., Department of Agriculture, Peradeniya, Ceylon. (1929.)
255. Parke Davis & Co., Medical Research Library, P.O. Box 488, Detroit, Michigan, U.S.A. (1920.)
256. Parker, Professor C. S., Department of Botany, Howard University, Washington, D.C., U.S.A. (1932.)
257. Pearson, Mr Arthur A., F.L.S., 59, Southwark Street, London, S.E. 1. (1911.)
258. Peklo, Dr Jaroslav, Professor of Applied Botany, Bohemian Technical University, Charles Square, Prague II, Czechoslovakia. (1924.)
259. Perthshire Society of Natural Science, c/o Mr James Winter (Hon. Treasurer), 35, George Street, Perth. (1919.)
260. Petch, Mr T., B.A., B.Sc., North Wootton, King's Lynn, Norfolk. (1911.)
261. Pethybridge, Mr G. H., Ph.D., B.Sc., F.L.S., Ministry of Agriculture, Pathological Laboratory, Milton Road, Harpenden, Herts. (1919.)
262. Peyronel, Dr Benjamino, R. Istituto Sup. Agrario e Forestale, Piazzale del Re, Firenze, Italy. (1932.)
263. Philadelphia, The Academy of Natural Sciences of Philadelphia, Nineteenth and The Parkway, Phil., U.S.A. (1925.)
264. Phillips, Dr H. H., 6, St John's Road, Penge, London, S.E. 10. (1923.)
265. Ping, Mr A. Wentworth, M.A., "St Olave's", Clifton, York. (1926.)

266. Plowright, Mr C. T. M., B.A., M.B., Darnick, Flore, Northampton. (1901.)

267. Potter, Rev. M. C., Sc.D., M.A., F.L.S., Corley Croft, New Milton, Hants. (1896.)

268. Preston, Mr N. C., B.Sc., Harper Adams Agricultural College, Newport, Salop. (1920.)

269. Pretoria, South Africa, The Chief, Division of Botany (91403), Department of Agriculture. (1922.)

270. Purdue University, Library, Agricultural Experiment Station, Lafayette, Ind., U.S.A. (1931.)

271. Pusa, Imperial Mycologist, Imperial Agricultural Research Institute, Pusa, Bihar, India. (1921.)

272. Ramsbottom, Mr J., O.B.E., M.A., F.L.S., British Museum (Nat. Hist.), Cromwell Road, South Kensington, London, S.W. 7. (1910.)

273. Ray, Miss Anne, Penarwyn, Gorran Haven, Gorran, Cornwall. (1929.)

274. Rayner, Dr M. Cheveley (Mrs Neilson Jones), Bedford College for Women, Regent's Park, London, N.W. 1. (1921.)

275. Rea, Miss M. W., M.Sc., Salem House, Sydenham, Belfast, Northern Ireland. (1920.)

276. Rees, Mr John, M.Sc., Adviser in Agricultural Botany, University College, Cardiff. (1929.)

277. Reichert, Dr Israel, Jewish Agency for Palestine, Agricultural Experiment Station, P.O.B. 15, Rehoboth, Palestine. (1924.)

278. Rhind, Mr Donald, B.Sc., Economic Botanist, Department of Agriculture, Agricultural College, Mandalay, Burma. (1922.)

279. Rhodes, Miss Mabel, Lister Institute, Chelsea Gardens, London, S.W. 1. (1921.)

280. Robson, Mr R., M.Sc., F.Z.S., East Hanningfield, Chelmsford, Essex. (1914.)

281. Roper, Miss Ida M., F.L.S., "The Curatage", 176, Chessell Street, Ashton Gate, Bristol 3. (1921.)

282. Rothamsted Experimental Station, Department of Mycology, Harpenden, Herts. (1923.)

283. Rutgers College and State University of New Jersey, Library, New Brunswick, New Jersey, U.S.A. (1922.)

284. St Paul, Minnesota, U.S.A., The Library, Department of Agriculture, University Farm. (1920.)

285. Salam, Mr M. M. Abdel-, Cotton Research Board, Giza, Egypt. (1930.)

286. Salisbury, Professor E. J., D.Sc., F.R.S., F.L.S., Botanical Department, University College, Gower Street, London, W.C. 1. (1921.)

287. Salmon, Professor E. S., F.L.S., South-Eastern Agricultural College, Wye, Kent. (1922.)
288. Sampson, Miss K., M.Sc., University College, Aberystwyth, North Wales. (1920.)
289. Samuel, Mr Geoffrey, M.Sc., Department of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts. (1923.)
290. Scott, Mr W. W., 13, Bishop's Road, Highgate, London, N. 6. (1922.)
291. Searle, Mr G. Odell, B.Sc. (Agric.), Research Botanist, Linen Industry Research Association, Glenmore House, Lambeg, Lisburn, Northern Ireland. (1920.)
292. Seth, Mr N. L., B.Sc., Ph.D., D.I.C., Agricultural College, Mandalay, Burma. (1930.)
293. Sharples, Mr A., A.R.C.S., D.I.C., c/o Messrs Grindlay & Co., Parliament Street, London, S.W. 1. (1924.)
294. Shaw, Mr F. J. F., D.Sc., A.R.C.S., F.L.S., Imperial Agricultural Research Institute, Pusa, Bihar, India. (1920.)
295. Shear, Dr C. L., U.S. Department of Agriculture, Bureau of Plant Industry, Washington, D.C., U.S.A. (1930.)
296. Small, Mr W., M.B.E., M.A., Ph.D., B.Sc., Director, Department of Agriculture, Zomba, Nyasaland. (1915.)
297. Smith, Mr Alexander, M.A., Ph.D., Ministry of Agriculture, Pathological Laboratory, Milton Road, Harpenden, Herts. (1924.)
298. Smith, Miss K. E., The Quarry, Lutterworth Road, Nuneaton. (1913.)
299. Smith, Professor Noel J. G., Ph.D., B.Sc., Botany Department, Rhodes University College, Grahamstown, S. Africa. (1924.)
300. Smith, Mr Rupert, 38, Greenhill Gardens, Edinburgh. (1927.)
301. South London Botanical Institute, 323, Norwood Road, Tulse Hill, London, S.E. 24. (1921.)
302. Stakman, Professor E. C., University of Minnesota, Department of Agriculture, University Farm, St Paul, Minn., U.S.A. (1922.)
303. Statham, Miss E. M., 2, Westbrook Road, Blackheath, London, S.E. 3. (1926.)
304. Stationery Office, H.M., Superintendent of Publications, Book Dept., Westminster, S.W. 1. (4 subscriptions.) (1920.)
305. Stephens, Miss E. L., B.A., Department of Botany, University of Cape Town, Cape Town, South Africa. (1928.)
306. Stephens, Miss F. L., M.Sc., Department of Botany, British Museum (Natural History), Cromwell Road, South Kensington, London, S.W. 7. (1930.)

307. Steyaert, M. R. L., Station de Sélection Cotonnière de Bambesa, District des Uélés, Belgian Congo. (1931.)

308. Stirrup, Mr H. H., M.Sc., Midland Agricultural College, Sutton Bonington, Loughborough. (1922.)

309. Storey, Mr H. H., M.A., Ph.D., East African Agricultural Research Institute, Amani, Tanganyika Territory, East Africa. (1922.)

310. Sutherland, Mr G. K., M.A., D.Sc., F.L.S., "Bremhill", 21, Combe Park, Bath, Somerset. (1914.)

311. Swansea Field Naturalists' Society, c/o Mr E. R. Brown, 71, Rhyddings Park Road, Swansea, South Wales. (1924.)

312. Swanton, Mr E. W., A.L.S., Educational Museum, Haslemere, Surrey. (1899.)

313. Swedish Academy of Sciences, Royal, Stockholm, Sweden. (1919.)

314. Sydney, Australia, The Librarian, University of. (1922.)

315. Sydow, Herr H., Luitpoldstrasse 33, Berlin, W. 30, Germany. (1931.)

316. Tabor, Mr R. J., B.Sc., F.L.S., Botanical Department, Imperial College of Science, South Kensington, London, S.W. 7. (1914.)

317. Taylor, Mr J. C., B.Sc., B.Agr., Department of Agricultural Botany, Queen's College, Belfast, N. Ireland. (1933.)

318. Telfer, Mr R. Allsop, 7, Christchurch Road, Worcester. (1931.)

319. Tennessee, University of, Agricultural Experiment Station, Library, Knoxville, Tennessee, U.S.A. (1926.)

320. Tervet, Mr I. W., B.Sc., c/o G. M. Tervet, Esq., 11, Whitehaugh Drive, Paisley. (1933.)

321. Tetley, Miss U., Quarry Garth, Windermere, Westmoreland. (1929.)

322. Tomkins, Mr R. G., M.A., Ph.D., Trinity College, Cambridge. (1925.)

323. Tunstall, Mr A. C., Tocklai Experimental Station, Cinnamara P.O., Assam, British India. (1933.)

324. United States Department of Agriculture, c/o Wheldon and Wesley, 2-4 Arthur Street, New Oxford Street, London, W.C. 2. (1907.)

325. Vaheeduddin Syed, Department of Plant Pathology, University Farm, St Paul, Minnesota, U.S.A. (1934.)

326. Vanterpool, Mr T. C., M.Sc., Botanical Department, University of Saskatchewan, Saskatoon, Canada. (1929.)

327. Vasudeva, Mr R. S., Cotton Pathologist, Agricultural College, Lyallpur, Punjab, India. (1929.)

328. Wadham, Professor S. M., M.A., Department of Agriculture, The University, Melbourne, Victoria, Australia. (1922.)
329. Wakefield, Miss E. M., M.A., F.L.S., Herbarium, Royal Botanic Gardens, Kew. (1911.)
330. Waldie, Mr J. S. L., B.Sc., C.D.A., Department of Agricultural Botany, The University, Reading. (1925.)
331. Wales, University College of, Librarian, Botanical Department, Aberystwyth, North Wales. (1927.)
332. Wallace, Mr E. R., Agricultural Institute, Kirton, nr Boston, Lincs. (1934.)
333. Wallace, Mr G. B., B.Sc. (Agric.), Ph.D., Department of Agriculture, Morogoro, Tanganyika Territory, East Africa. (1928.)
334. Wallace, Mrs G. B., B.Sc., Morogoro, Tanganyika Territory, East Africa. (1924.)
335. Wallis, Mr A., Westacre, Station Road, Kettering. (1921.)
336. Ware, Mr W. M., D.Sc., South-Eastern Agricultural College, Wye, Kent. (1924.)
337. Washington, Library, State College of, Pullman, Washington, U.S.A. (1924.)
338. Waterston, Mr J. M., B.Sc., The Botany School, Cambridge. (1934.)
339. Watson, Mr W., D.Sc., A.L.S., Cedene, Cheddon Road, Taunton. (1933.)
340. Welsmann, Dr Ludwig, Pelkum, bei Hemm, Westphalia, Germany. (1932.)
341. Westerdijk, Professor Johanna, Javalaan 4, Baarn, Holland. (1923.)
342. Western, Mr J. H., B.Sc., Department of Agricultural Botany, University College of Wales, Aberystwyth. (1934.)
343. Weston, Mr W. A. R. Dillon, M.A., School of Agriculture, Cambridge. (1923.)
344. Whetzel, Professor H. H., M.A., New York State College of Agriculture, Cornell University, Ithaca, N.Y., U.S.A. (1914.)
345. Whitaker, Mr F. Owen, 51, Grosvenor Avenue, Carshalton, Surrey. (1921.)
346. Whitehead, Mr T., D.Sc., A.R.C.S., University College of North Wales, Bangor. (1920.)
347. Wilkins, Mr W. H., M.A., Department of Botany, The University, Oxford. (1928.)
348. Williams, Mr P. H., 4, Belmont Villas, Windmill Lane, Cheshunt, Herts. (1930.)
349. Wilson, Miss A. P., M.B.E., A.R.C.S., 116, Fellows Road, London, N.W. 3. (1929.)

350. Wilson, Mr Alastair R., B.Sc., The Botany School, Cambridge. (1933.)

351. Wilson, Mr Malcolm, D.Sc., A.R.C.S., F.L.S., Royal Botanic Garden, Edinburgh. (1921.)

352. Wiltshire, Mr S. P., M.A., Imperial Mycological Institute, Ferry Lane, Kew, Surrey. (1920.)

353. Wisconsin, The Library, University of, Madison, Wis., U.S.A. (1923.)

354. Wolf, Mr B. L., N.D.A., Cornwall Buildings, 45, Newhall Street, Birmingham. (1923.)

355. Woodcock, Mr A. J. A., M.Sc., F.E.S., Rhianva, 65, Rock Avenue, Gillingham, Kent. (1926.)

356. Woodward, Mr R. C., Ph.D., Imperial Chemical Industries, Ltd., Millbank, London, S.W. 1. (1924.)

357. Woolhope, The Naturalists' Field Club, Hereford. (1896.)

358. Worcestershire Naturalists' Field Club, c/o Mr W. J. Else, Victoria Institute, Worcester. (1921.)

359. Wormald, Mr H., D.Sc., A.R.C.S., Research Station, East Malling, Kent. (1921.)

360. Wright, Mr E. Barton, M.Sc., Scottish Society for Research in Plant Breeding, Craig's House, Corstorphine, Midlothian. (1926.)

361. Yale University, Library, New Haven, Connecticut, U.S.A. (1930.)

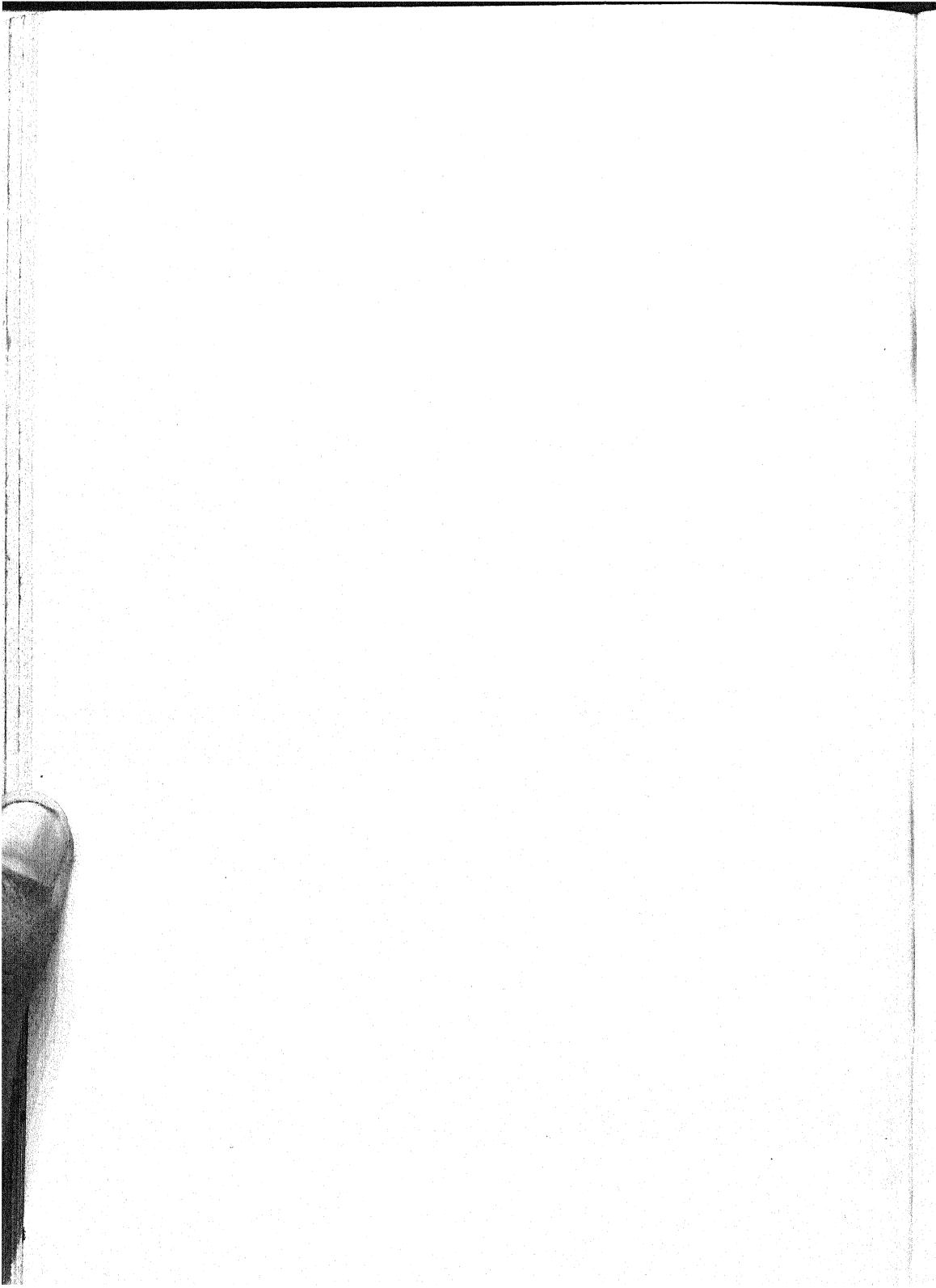
362. Yeoman, Mr J. B., M.D., Norton, Wirral, Cheshire.

363. Young, Miss Elaine M., Ph.D., M.Sc., University of the Witwatersrand, Johannesburg, South Africa. (1927.)

364. Zundel, Dr G. L. I., Botany Building, Pennsylvania State College, State College, Pa., U.S.A. (1929.)

365. Zürich, Switzerland, Botanical Garden and Museum, c/o Dr A. U. Däniker. (1921.)

366. Zürich, Institut für Spezielle Botanik der Eidg. Techn. Hochschule. (1928.)



## RULES

### *Society's Name and Objects*

1. The Society shall be called "The British Mycological Society", and its object shall be the study of Mycology in all its branches.

### *Members of Society*

2. The Society shall consist of Honorary Members, Foundation Members and Ordinary Members; the number of Honorary Members shall be limited to 20, and that of Foundation Members to 100, but the number of Ordinary Members shall be unlimited.

### *Honorary Members*

3. Honorary Members shall be persons of pre-eminence in Mycology, or who have rendered special service to the Society.

### *Foundation Members*

4. Foundation Members shall be those Members or Societies who joined the Society previous to the limit of 100 Members having been attained.\*

### *Officers*

5. The Officers of the Society shall consist of a President, one or more Vice-Presidents, Treasurer, Secretaries, and Editor or Editors. They shall be elected annually, at the Annual General Meeting of the Society.

### *Government of Society*

6. The government of the Society shall be vested in a Council, which shall consist of the President and other Officers for the time being, together with two or more other Members who shall be elected annually at the General Meeting, and one-half of whom shall retire each year and not be eligible for immediate re-election. The Members to retire shall be those who have been longest in office or, in case of equality, shall be determined by ballot. Ex-Presidents are *ex-officio* Members of the Council.

Every Meeting of the Council shall be duly summoned by the Hon. Secretary by at least seven days' notice in writing to each Member of the Council.

### *Period of Office*

7. The Officers and Council shall hold office as from the 1st of January following their election.

\* The limit of 100 Foundation Members was reached 22nd October, 1903.

*Plant Pathology Committee*

8. The special interests of Plant Pathology shall be delegated to an executive committee, to be called the Plant Pathology Committee of the British Mycological Society. This Committee shall consist of the President and Secretaries *ex-officio* and twelve other members of the Society. The latter shall be elected annually at the Annual General Meeting of the Society, and one-quarter shall retire in rotation each year and shall not be eligible for immediate re-election. The members to retire shall be those who have been longest in office, or, in case of equality, shall be determined by ballot.

The Officers shall consist of a Chairman and a Secretary, to be elected by the Committee each year.

At least two meetings shall be held every year, six members to form a quorum.

The Committee shall have power to appoint for any special purpose a sub-committee consisting either wholly or partly of members of the Committee.

*Election of Members*

9. Honorary Members shall only be elected at a Meeting of the Society by a majority of the Members then present.

All Ordinary Members shall be proposed and seconded respectively by existing Members, who shall sign a certificate (see Appendix) of recommendation, one at least of the proposers so certifying from personal knowledge. Every candidate for election shall sign an undertaking to abide by the Rules if elected (see Appendix). They shall be elected by a majority of the Members present at any meeting of the Society or by the President and Officers of the Society.

*Subscription*

10. All Ordinary Members and Societies shall pay an annual subscription of one pound, and Foundation Members five shillings, due on the 1st of January in each year. Honorary Members shall be exempt from any annual subscription.

Any Member wishing to retire from the Society shall give notice to the Hon. Secretary or Treasurer in writing before the 1st of December of the previous year.

*Meetings*

11. The Society shall hold one or more meetings annually, at a place and time determined by the Members at the preceding Annual General Meeting, or by the Council. The Annual General Meeting, for the election of officers and the transaction of other business, shall coincide with the Autumn Foray.

*Accounts*

12. At the Annual General Meeting of the Society in each year the Hon. Treasurer shall present duly audited accounts.

*Alteration of Rules*

13. The Rules shall not be altered except by a two-thirds majority of the Members present at an Annual General Meeting. A printed copy shall be sent to every Member of the Society on election, and in the event of alterations to all Members.

**APPENDIX***Form of proposal for Ordinary Membership of the British  
Mycological Society*

of.....

being desirous of becoming an Ordinary Member of the British Mycological Society, we, the undersigned Members of the Society, certify that we consider h..... to be a desirable Member of the Society, and beg to recommend h..... for election.

Dated this ..... day of ..... 19.....

.....(From personal knowledge.)

*Certificate to be signed by the Candidate*

I hereby certify that I desire to become an Ordinary Member of the British Mycological Society and that I will abide by the Rules if elected.



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